Neural Mechanisms of Self-Control Exertion

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by

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„The only way to get rid of temptation is to yield to it.“

Oscar Wilde, *The Picture of Dorian Gray*

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Abstract

Abundant research from social psychology suggests that self-control weakens temporarily if individuals have to control themselves repeatedly. The consequences of exerted self-control have become known as depletion effects, yet the mechanisms behind these effects are poorly understood. Several models have been proposed, either focusing on depletion of a self-control resource or on motivational changes. This background provides an ideal starting position to adopt established study designs for neuroscientific investigations. Learning about the neural correlates of self-control exertion has the potential to advance our understanding of self-control exhaustibility and self-control in general. In my PhD project, I examined self-control exertion effects with three fMRI studies. The first study replicated findings that the negative consequences of self-control exertion can be overcome by increasing task motivation on the behavioral level. Yet on the neural level, effects of depletion and motivation had interacting effects on brain activity. This supports the assumption of a self-control resource, and contradicts alternative motivational models of depletion. In the second study, effects of effortful emotion regulation on a subsequent resting state were measured, which allowed to examine effects of self-control exertion in the absence of task engagement. Emotion suppression led to connectivity increases between regulatory and task-specific areas beyond task duration, which was related subjective exhaustion. We propose depletion effects might be associated with a reduced capacity of regulatory brain areas to influence further regions and thus control processing of new effortful tasks. The third study built on findings which suggested that depletion strengthens emotional experiences. It was assumed that depletion should also have beneficial effects on emotional memory formation. Unfortunately, we were unable to replicate findings of increased emotional processing after self-control exertion. Thus our hypothesis about a connection between depletion and emotional memory could not be tested. This

and other null findings are reflected in a series of recent meta-analyses, which suggest that the depletion effect may be smaller in magnitude than has been assumed. In sum, this PhD project provides unparalleled evidence for lingering neural effects of self-control exertion which are most compatible with self-control resource assumptions. While the physiological basis of the self-control resource remains elusive, the present results suggest that self-control exertion might temporarily reduce the capacity of regulatory brain centers, such as the inferior frontal gyrus, to adjust to new self-control demands.

Zusammenfassung

Zahlreiche Studien aus der Sozialpsychologie zeigen dass Selbstkontrolle vorübergehend schlechter wird bei wiederholter Ausübung. Die Konsequenzen von Selbstkontrollerschöpfung wurden bekannt als „Depletioneffekte“, die Gründe dafür sind jedoch unklar. Verschiedene Modelle wurden aufgestellt, welche entweder auf der Erschöpfung einer Selbstkontrollressource oder auf motivationalen Veränderungen basieren. Dies ist eine ideale Ausgangslage um etablierte Untersuchungsdesigns für neurowissenschaftliche Studien zu adaptieren. Neues Wissen über die neuronalen Korrelate von Depletioneffekten zu gewinnen könnte auch unser generelles Verständnis von Selbstkontrolle und deren Erschöpfbarkeit entscheidend vorantreiben. In meinem Dissertationsprojekt habe ich Depletioneffekte in drei fMRI-Studien untersucht. Die erste Studie replizierte Befunde, dass gesteigerte Motivation den Leistungseinbrüchen nach Depletion entgegenwirken kann. Dabei konnten wir erstmals aufzeigen, dass die Auswirkungen von Depletion und Motivationsveränderungen auf der Gehirnebene interagieren. Das spricht für die Annahme einer Selbstkontrollresource, und widerspricht alternativen motivationalen Erklärungsansätzen zu Depletion. In der zweiten Studie wurden die Effekte einer anstrengender Emotionsregulation auf eine anschliessende Erholungsphase („resting state fMRI“) gemessen. Dies erlaubte die Untersuchung von Selbstkontrollerschöpfungseffekten ohne weitere Taskanforderungen. Emotionsunterdrückung führte zu einer Konnektivitätsteigerung zwischen regulierenden und Task-spezifischen Arealen, welche länger als der Task anhielt und mit subjektiver Erschöpfung zusammenhing. Wir schlagen vor, dass Depletioneffekte assoziert mit einer verminderten Fähigkeit von Regulationsarealen weitere Gehirnareale zu beeinflussen und die Verarbeitung eines neuen Tasks zu kontrollieren. Die dritte Studie war inspiriert von Experimenten, welche suggerierten dass Depletion die emotionale Verarbeitung verstärkt. Wir gingen zusätzlich davon aus

dass sich Depletion förderlich auf die emotionale Gedächtnisbildung auswirken sollte. Leider konnten wir die Auswirkungen von Depletion auf die emotionale Verarbeitung nicht replizieren. Somit konnten wir auch unsere Hypothese, den Bezug von Depletion zu emotionalem Gedächtnis, nicht testen. Dieser und andere Nullbefunden decken sich mit neuen Meta-Analysen, welche besagen dass die Stärke des Depletioneffekts schwächer sein dürfte als bisher angenommen wurde. Diese Doktoratsarbeit legt neue Evidenz vor, dass Selbstkontrollerschöpfung nachhallende Effekte auf die Hirnaktivität hat, welche am besten mit Ressourcenerschöpfung zu erklären sind. Während die physiologische Basis der Selbstkontrollressource unklar bleibt, deuten die Ergebnisse an, dass Selbstkontrollerschöpfung mit einer vorübergehenden verringerten Fähigkeit von regulierenden Hirnarealen wie dem Gyrus frontalis inferior zusammenhängt, an neue Selbstkontrollanforderungen zu adaptieren.

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1 Background

1.1 Introduction

Self-control, sometimes also called willpower or self-regulation, is the ability to control thoughts, emotions and impulses. It is needed to inhibit dominant responses and desires associated with immediate reward in order to align behavior with long-term goals, or other personal or societal standards. For example, if somebody wanted to stop smoking, self-control is needed to resist the temptations arising from seeing other people smoking. Self-control failure is strongly connected with health-related issues, such as sexually transmitted diseases, physical inactivity, obesity and eating disorders, and abuse of tobacco, alcohol, and other substances (Baumeister & Heatherton, 1996). It is estimated that around 40% of premature, preventable deaths are caused by behavioral factors, mainly smoking and physical inactivity (Schroeder, 2007). Self-control furthermore predicts social, educational, and economic success (Mischel, Shoda, & Rodriguez, 1989; Moffitt et al., 2011). In fact, self-control is one of the psychological constructs with the highest predictive power for life outcomes in general, comparable to intelligence or socioeconomic status (Duckworth, 2011). Hence psychological research has invested great efforts in understanding the processes and mechanisms leading to self-control failures (e.g. Hagger, Wood, Stiff, & Chatzisarantis, 2010; Hare, Camerer, & Rangel, 2009; Inzlicht, Schmeichel, & Macrae, 2014).

In the past 20 years, a lot of research in social psychology has investigated conditions which contribute to self-control failure. Over 200 experiments have found that individuals are worse at self-control when they exerted self-control previously (Carter, Kofler, Forster, & McCullough, 2015; Hagger et al., 2010). The traditional model assumes that self-control depends on a limited resource, which becomes depleted by use (Baumeister

& Heatherton, 1996; Baumeister, Vohs, & Tice, 2007). Yet this model has been challenged in recent years by theories which assume depletion effects are related to changes in motivation, not resources (Inzlicht et al., 2014; Kool & Botvinick, 2014; Kurzban, Duckworth, Kable, & Myers, 2013).

Contrasting abundant behavioral studies, hardly any brain imaging studies on self-control exertion effects were published at the beginning of this PhD project and there are still very few today (Friese, Binder, Luechinger, Boesiger, & Rasch, 2013; Persson, Larsson, & Reuter-Lorenz, 2013; Wagner, Altman, Boswell, Kelley, & Heatherton, 2013; Wagner & Heatherton, 2013). Yet learning about the neural correlates of self-control exertion provides various opportunities to examine the effects of self-control exertion which could not be achieved by behavioral studies alone, potentially making significant contributions to the ongoing debate about the mechanisms behind self-control exertion effects.

This is a cumulative thesis with three manuscripts for publication. The introductory first section will provide an overview of research on self-control and self-control exertion, presenting different models of self-control exertion. A general framework for the neural correlates of self-control will be laid out, followed by a more detailed look at neuroscientific depletion studies. An overview of behavioral and neuroscientific research on emotion regulation is presented as it is closely connected to self-control. The introduction will conclude with the deduction of the research question we sought to answer with our studies. The second section contains the publication manuscripts describing the conducted studies. The last section presents a conclusive discussion of these empirical findings.

1.2 Behavioral research of self-control and self-control exertion

In a classic experiment, a marshmallow was presented to four to five year-old children (Mischel et al., 1989). The children were left alone and were told they would receive a second marshmallow if they managed not to eat until the experimenter returned (approx. 15 min later). The longer the preschool children were able to resists the sweets, the better were their school grades and social skills 15 years later, and the lower was their body mass index 30 years later (Schlam, Wilson, Shoda, Mischel, & Ayduk, 2013). These findings have been interpreted as a strong indicator for the important role of self-control over the lifespan, yet they have also been criticized for not controlling for potential confounds such as socioeconomic status or intelligence (e.g. Kidd, Palmeri, & Aslin, 2013). A newer study of a complete birth cohort of a town in New Zealand examined the influence of self-control measured within the first ten years of life while controlling for intelligence and socioeconomic status statistically (Moffitt et al., 2011). Self-control predicted psychological and physical health, financial autonomy, criminality and substance abuse more than 20 years later. These two studies provide convincing evidence for the life-spanning predictive power of self-control.

In addition to studies of individual differences in self-control, social-psychological researchers have broadly examined short-term changes in self-control and consistently reported that controlling oneself increases chances of subsequent self-control failure (Hagger et al., 2010). This line of research is greatly inspired by the strength model from Baumeister and colleagues (Baumeister & Heatherton, 1996; Baumeister et al., 2007). This model makes two assumptions: First, there is a domain-general self-regulatory strength. This suggests that a person who is e.g. good at resisting sweets is also good at other forms of self-control such as staying calm under emotional stress. The second assumption is that that self-control strength depends on a limited resource. Self-control has

been compared to a muscle, which gets tired with use, but profits from training and regenerates over time (Muraven & Baumeister, 2000). The supposed resource is also thought to become depleted with use. The resulting state of reduced self-control strength makes self-control failure more likely and has been dubbed depletion or ego-depletion. These terms will be used as synonyms for self-control exertion, unrelated to any theoretical frameworks.

These temporary effects of self-control exertion are typically investigated using a dual-task paradigm. Participants complete a first task in one of two conditions, which are either demanding self-control, thus inducing depletion, or not demanding self-control. All participants subsequently engage in the same second self-control task. The expected outcome is that participants, who exerted self-control in the first task, perform worse on the second. In one study, in the first task all participants were exposed to the smell and sight of freshly baked cookies, but only half could try them (control group), whereas the other half was instructed to resist them and instead eat radishes (depletion group). The second task consisted of an unsolvable puzzle. Participants in the depletion group gave up sooner on the puzzle than participants in the control group (Baumeister, Bratslavsky, Muraven, & Tice, 1998). Depletion effects have been demonstrated in very diverse contexts. After exerting self-control, individuals performed worse at working memory tasks (Schmeichel, 2007), took more risks (Freeman & Muraven, 2010), regulated emotions less successfully (Muraven, Tice, & Baumeister, 1998; Wagner & Heatherton, 2013), ate more unhealthy food (Vohs & Heatherton, 2000), and were more likely to show sexually inappropriate or aggressive behavior (DeWall, Baumeister, Stillman, & Gailliot, 2007; Gailliot & Baumeister, 2007a). Smokers smoked more after self-control exertion (Shmueli & Prochaska, 2009).

Hagger et al. (2010) conducted a meta-analysis of 198 experiments which examined depletion effects with the dual-task paradigm. The authors reported an overall effect size of d = 0.62 (Confidence Interval [0.57, 0.67]) for self-control performance, which indicates a moderate-to-large effect (Cohen, 1988). In addition, self-control exertion induced significant changes in effort, perceived difficulty, negative affect, subjective fatigue, and blood glucose levels. Moderator analyses favored the assumption of a domain-general self-control strength. Hagger et al. (2010) concluded that the findings support the view that self-control draws from a single, global, depletable resource and that the strength model is a useful explanatory framework for self-control. However, the authors also added that the mechanisms underlying depletion effects are not well understood, and that other explanations, such as changes in motivation or fatigue, exist.

One of the major challenges of the strength model is that the supposed self-control resource has never been measured directly, but instead its existence is inferred from the effects found in the dual-task paradigm. It is unclear what the limited resource actually is. Baumeister's group suggested that glucose is the limited energy source for self-control (Gailliot & Baumeister, 2007b; Gailliot et al., 2007). In a series of dual-task experiments, they found that self-control tasks lowered blood glucose levels, and that low glucose levels after the first task predicted poor performance on the second task. Consuming a glucose drink in between tasks eliminated the depletion effect. However, these findings have been heavily criticized. Kurzban (2010) argues that cognitive tasks have very little effect on brain metabolism and overall glucose consumption. It is biologically highly implausible that a measureable effect in blood glucose levels would appear (Raichle & Mintun, 2006). Furthermore, Kurzban (2010) reanalyzed the data from Gailliot et al. (2007) and rejected the evidence that self-control tasks lower blood glucose significantly. Another study failed

to replicate the finding that self-control tasks lowered blood glucose and found that rinsing, but not ingesting, the mouth with a sugary drink bolstered self-control (Molden et al., 2012). The "gargle effect", i.e. rinsing the mouth with sugar to enhance self-control, has been interpreted as a strong indicator for the involvement of motivational factors in self-control (Molden et al., 2012; Sanders, Shirk, Burgin, & Martin, 2012). These findings render the original glucose hypothesis of self-control hard to defend.

Beedie and Lane (2012) combined motivational factors and limited glucose in a new model of resource allocation. Differing from Kurzban's (2010) conclusions, the authors argued that engaging in an effortful self-control task might indeed use bigger amounts of glucose and consequently lower the local availability of glucose. However, as there is more than enough glucose in the blood, the body is readily able to compensate by supplying more blood to the brain area in need. Blood flow is suggested to depend on personal priorities. Thus, only if task motivation is high, enough glucose will be supplied to areas critically involved in task processing for optimal functioning.

Besides gargling, a number of further moderators of depletion effects have been identified, which point towards the importance of psychological factors. For example, meditation (Friese, Messner, & Schaffner, 2012), affirmation of core values (Schmeichel & Vohs, 2009), or induction of a positive mood (Tice, Baumeister, Shmueli, & Muraven, 2007) has been shown to counteract the deleterious effects of depletion on subsequent self-control performance. Even lay theories about willpower influence self-control (Job, Dweck, & Walton, 2010). Participants who viewed self-control as an unlimited capacity did not show the usual performance drop after self-control exertion.

A prominent study examined the moderating role of motivation on self-control (Muraven & Slessareva, 2003). They boosted motivation in half of the participants by letting them believe that the second task would help others, that their efforts could benefit

them, or by providing a monetary compensation for their performance in the second task. Participants who were motivated by any of these manipulations did not show decrements in task performance after self-control exertion. The authors suggested that the results confirm a moderator role of motivation in self-control. Ego-depletion may render subsequent attempts at self-control more difficult and more effortful, thus additional motivation is needed to keep participants engaged in the task. Muraven and Slessareva (2003) also outlined what would later become known as the resource conservation principle (Muraven, Shmueli, & Burkley, 2006). The idea is that individuals are motivated to conserve self-control strength, especially if self-control strength has already been partially depleted. This is an important clarification of the strength model (Baumeister & Vohs, 2007), depletion effects may thus not only occur when the resource is completely gone, but also when it is partially depleted. As a comparison, imagine you are on a hike and have one bottle of water with you. You will try to save water the harder the less there is left in the bottle.

In sum, research has amply demonstrated the significance of self-control in human life. Behavioral experiments have shown temporal decrements in self-control in various contexts. These depletion effects have been linked to a self-control resource, but the physiological basis of the resource is unclear. Various moderators of depletion effects have been identified, e.g. participants' task motivation.

1.3 Different models of self-control exertion

Question have emerged about the existence of a specific self-control resource. Especially the finding that motivation can "undo" self-control exertion has led some researchers to argue that depletion effects are due to a loss of motivation instead of resource

exertion. This chapter will provide an overview of three alternative explanatory frameworks for depletion effects and also report the most recent reactions from Baumeister (2014) favoring a resource approach.

Process model

Inzlicht and Schmeichel (2012) were among the first who argued against the existence of a self-control resource and instead postulated that engaging in effortful self-control leads to temporary shifts in motivation, attention, and emotion. According to the process model (Inzlicht et al., 2014; Inzlicht & Schmeichel, 2012), individuals seek to balance externally rewarded cognitive labor and leisure. Cognitive labor has an inherent disutility which accumulates during continued work. As a consequence, a motivated switching occurs where individuals start to strive for inherently rewarding leisure. From an evolutionary perspective, this is related to finding an optimal trade-off between exploitation of known resources (labor), and disengagement and exploration of other activities which may be more gratifying (leisure). Consequently, the process model assumes that depletion is not simply less motivation overall. Rather, it is lower motivation to engage in "have-to" tasks and higher motivation to engage in "want-to" tasks. The shift in motivational priorities is accompanied by changes in attention and emotion. Signals for inherently rewarding leisure become more salient and associated emotions are experienced more intensively, while stimuli signaling cognitive labor are paid less attention and become increasingly aversive on an emotional level. One may critically add that changes in attention and emotion could also be explained by a decreased self-control capacity, as assumed by the strength model. One might also question the functionality of task disengagement during a standardized laboratory experiment where chances for alternative, more rewarding activities are obviously very low.

Opportunity cost model

Kurzban, Duckworth, Kable, and Myers (2013) reject the resource concept in favor of subjective costs. Computational mechanisms or mental operations such as executive functions, can be deployed for various tasks, but they can only be deployed for a limited number of simultaneous tasks at any given moment. Importantly, this model introduces opportunity costs. These are other potential uses of the computational mechanisms which cannot be executed during task engagement. Individuals are constantly evaluating the costs and benefits associated with task performance and the subjective experience of effort equals the felt output of these cost/benefit computations, which increases with time spent on task. Consequently, individuals' motivation for further deployment of computational mechanisms in service of the present task decreases over time, leading to performance reductions. While this model is formally explicit, it has been criticized that it fails to give an adequate reason why the evaluation of opportunity costs should rise with repetition (Cohen & Saling, 2013). Others have argued that the subjective value of alternative computational mechanisms should only change over time if task demands are previously unknown. Otherwise, effort will depend on previous task experience (Gendolla & Richter, 2013). As an explanation for task disengagement over time, Kurzban et al. (2013) use the following analogy: „[F]oraging animals [...] can feed in only one patch at any given time and, therefore, must decide when to stay in their current patch and when to leave it in search of new one [...] When foraging organisms change location, they do so because the rate of return falls below some threshold." (p. 664). Ironically, this is exactly the description of a resource problem. The decision to change locations is based on the availability of food, i.e. a resource. The relationship between costs and benefits becomes less favorable *because* the resource becomes sparse.

Labor/leisure tradeoff model

Kool and Botvinick (2013, 2014) propose that the exertion of cognitive control/self-control carries intrinsic subjective costs. Instead of limiting resources, they argue that self-control failures occur because individuals choose not to invest effort. This is similar to Kurzban et al.'s (2010) idea in that it centers on subjective costs, but the evaluation of these costs is directly attached to the exertion of cognitive control. The more control is needed, the higher are the subjective costs. Over time, individuals seek a balance between tasks requiring control and task disengagement or rest. This research group has focused more on neuroscience than other self-control researchers. Kool and Botvinick (2013, 2014) were able to present a neural analogue for subjective costs (Botvinick, Huffstetler, & McGuire, 2009). In an fMRI study, the response of the nucleus accumbens to a fixed reward value was smaller if it was attached to a high-demanding task than a low-demanding task. Furthermore, the decrease in the nucleus accumbens correlated with activation of the ACC during the preceding task. Thus the researchers argued the ACC may not only monitor task-processing with respect to potential conflicts, but monitor more generally information-processing demands. In another fMRI study by this research group, participants had to decide repeatedly between a high-demanding and a low-demanding task (McGuire & Botvinick, 2010). The higher the activity was in the left IFG during the high-demanding task, the more likely participants were to avoid it later. As the authors themselves noted, these results can also be interpreted in line with the strength model. Prior task engagement could have caused self-control exertion. Hence participants chose the less-demanding task because of resource depletion. As a counter argument, Kool & Botvinick (2014) conducted a behavioral experiment where participants also showed demand avoidance if they had to decide about task engagement prospectively. This implies that demand avoidance is not an emergent feature which follows resource

depletion. However, according to the resource conservation principle of the strength model (Muraven et al., 2006) participants might be motivated to spend as little of the self-control resource as possible, even if they had not engaged in self-control acts previously. Furthermore, from an evolutionary point of view, why would individuals feel a subjective cost for self-control if it did not, in the end, depend on a limited resource? Regarding this issue, Kool and Botvinick (2014) make two claims. First, the costs might stem from the limits of simultaneous information processing. Less demanding tasks leave more space for other mental activities. Second, task disengagement allows individuals to survey or explore potential alternative activities, thereby preventing focus on suboptimal behavior over an extended period of time. These points closely resemble the arguments outlined by the opportunity cost model (Kurzban et al., 2013) and the process model (Inzlicht et al., 2014).

Reaction to critique and overhaul of the strength model

An empirical argument against motivational accounts of depletion effects was provided by Vohs, Baumeister, and Schmeichel, (2013). They showed that increasing task motivation could counteract moderate amounts of self-control exertion, i.e. when participants completed one initial self-control task. When participants completed three initial self-control tasks, performance on the dependent task decreased further, and, critically, motivating participants had no beneficial effect on performance any more. The authors argue that motivation indeed plays a role in depletion effects, but cannot counter severe states of resource depletion. Baumeister (2014) also reacted to the critiques of the glucose hypothesis (see chapter 1.2) by acknowledging that "it seems unlikely that ego depletion's effects are caused by a shortage of glucose in the blood stream." (p. 315). Instead, he integrated the resource allocation model (Beedie & Lane, 2012), which is in line with

the resource conservation principle, into the strength model. Thus depletion effects occur because individuals decide not to devote an adequate amount of the stored glucose resources to a task. Baumeister (2014) furthermore emphasized that the selective allocation of a resource only makes sense if the resource is limited and can be depleted eventually. With respect to the "gargle effect" (i.e. boosting self-control by gargling glucose; Sanders et al., 2012), Baumeister (2014) points out that a small part of glucose is already metabolized in the mouth. This might be taken as a clue by the human body that more glucose is coming, which lowers the need to conserve the resource. On the downside, the strength model remains silent on how glucose storage, shortage, and allocation translates to a physiological or neural level.

Three models explaining self-control exertion effects in a motivational framework have been introduced. Inzlicht and Schmeichel (Inzlicht & Schmeichel, 2012) argued that participants strive for a balance between labor and leisure, which is perturbed after self-control exertion. Kurzban et al. (2013) and Kool and Botvinick (2013, 2014) emphasized the importance of value-based decision making for self-control, and agree that the driving force behind self-control exertion effects are subjective costs. These models struggle to explain why motivation decreases with increasing time spent on self-control demanding tasks. The strength model has been overhauled. Baumeister (2014) reiterated that the limited energy source relies on glucose, but added that the human body has extensive stores of glucose. Individuals try to conserve glucose by selective allocation and by increasing resistance to further allocation with increasing levels of depletion.

1.4 Neural correlates of self-control

The term "self-control" has only emerged in the neuroscientific literature in recent years (Heatherton & Wagner, 2011; Tabibnia et al., 2011). Yet neuroscientists have studied related concepts such as cognitive and executive control, interference or conflict resolution and even inhibition extensively. The prefrontal cortex (PFC) plays a critical role in these processes. It is this area of the brain which orchestrates thoughts and actions in accordance with internal goals. It is believed that the PFC maintains patterns of neural activity that represent goals and means to achieve them (Miller & Cohen, 2001). Through its rich interconnections with all sensory systems, the motor system, and subcortical structures involved in affect and memory, the PFC is thought to bias processing in the other parts of the brain in favor of goals. A renowned analogy is that the PFC exhibits top-down control over other brain areas and behavior. I will continue this chapter with a description of frequently used cognitive control tasks. Then common brain activity during cognitive tasks will be presented. Next, I will highlight how the tasks differ on the cognitive level and relate these differences and the respective mental operations to task-specific brain activity. Finally, I will argue that inhibition is the mental operation which is most directly related to self-control and discuss its neural basis further. This approach follows the logic introduced by an insightful meta-analysis by Nee, Wager, and Jonides (2007).

Go/no-go task. The task consists of a series go-signals and no-go signals (Fig. 1.a). Participants are required to respond as quickly as possible to go-signals but to withhold responding to no-go signals. Because the majority of trials consist of go-signals, a prepotent tendency to respond is formed.

Stop-signal task. On each trial, a Go-signal is presented (Fig. 2.a). Participants are instructed to press a button as quickly as possible whenever the Go-signal appears. In a

minority of trials, a stop signal is delivered after the go signal, e.g. an additional visual input or a tone. Participants must then cease executing an already initiated response. The time between the go and the stop signal is usually systematically varied until participants succeed stopping the response in 50% of trials.

Flanker task. In this task, several stimuli appear at once (Fig. 1.c). Participants must only respond to the target stimulus in the middle of the screen, while the stimuli to the side "flanking" the target stimuli have to be ignored. In incongruent trials, flanking stimuli cause interference because they are also potential targets but would require a different response. In congruent trials, flanking stimuli are the same as the target stimulus, thus facilitating processing. In neutral trials, flanking stimuli are left out or are stimuli without a response mapping.

Stroop task. Participants must indicate the color of the ink of letters appearing on screen while ignoring the meaning of the word (Fig. 1.d). In congruent trials, the meaning of the word and color of the ink match, e.g. "green" written in green ink. Task processing is facilitated and participants usually respond fast. In incongruent trials, the meaning of the word interferes with the ink color, e.g. "red" written in green ink. Incongruent trials usually elicit slower response times and more errors. Neutral trials consist of a word without a reference to colors or just letters, e.g. "XXX".

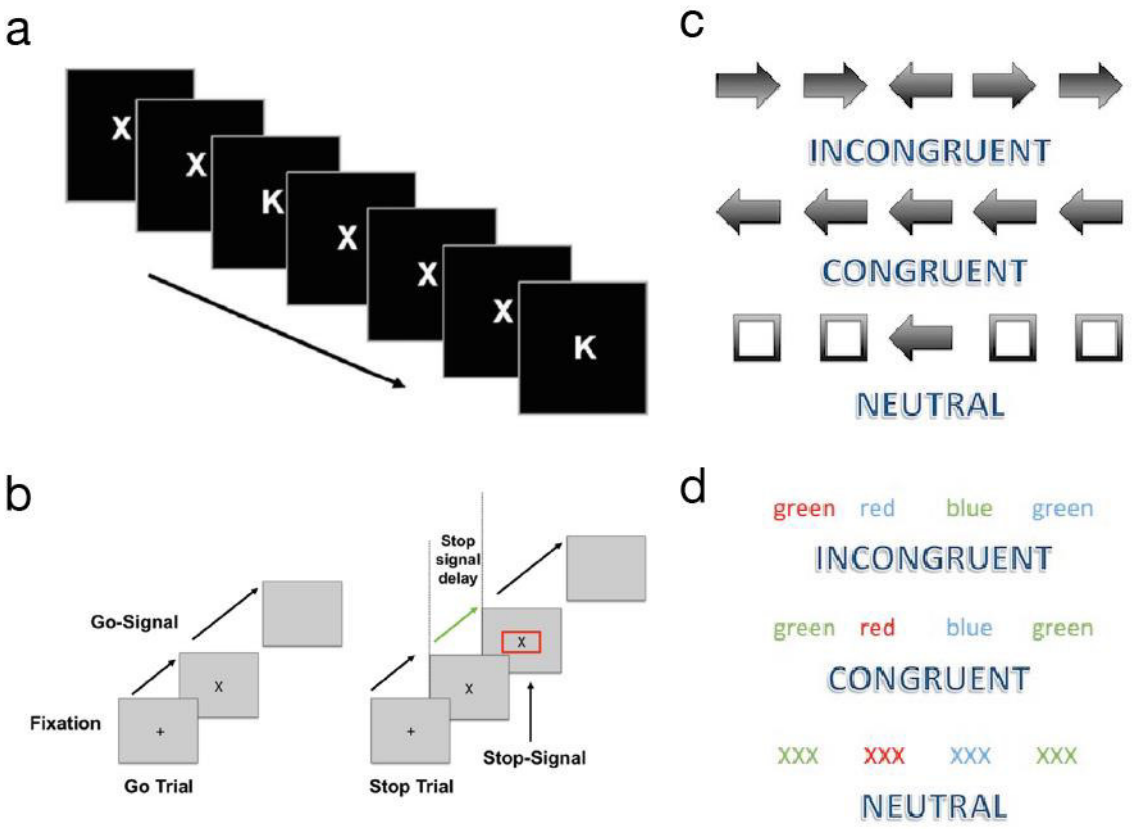

Fig. 1. Tasks commonly used in cognitive control research. (a) Go/no-go task. X, go trials; K, no-go trials. Adapted from "Neuroprediction of future rearrest" by E. Aharoni et al., 2013, *PNAS*, 110, p. 2 of Supporting Information. (b) Stop-signal task. X, go signal; red square, stop signal. Adapted from "Strength in cognitive self-regulation" by A. Barutchu, O. Carter, R. Hester, and N. Levy, 2013, *Frontiers in Psychology,* 4, p. 3. (c) Flanker task. Retrieved August 5, 2015 from https://en.wikipedia.org/wiki/Eriksen_flanker_task. (d) Stroop task.

As previously announced, I will now present general activity patterns related to cognitive control before revisiting each task and discuss the task-specific brain activity in light of different task demands. The meta-analysis by Nee, Wager, and Jonides (2007) implemented a density analysis to identify brain activation patterns based on 47 experiments with the described cognitive control tasks, plus two others (Simon task & stimulus-response compatibility). When combining all tasks, significant activation clusters were found bilaterally in the dorsolateral prefrontal cortex (DLPFC), inferior frontal gyrus (IFG, sometimes also referred to as ventrolateral prefrontal cortex), anterior cingulate cortex

(ACC), insula, and posterior parietal cortex. The authors also performed density analysis to examine brain activity related to each task separately, assuming that differences in brain activity relate to the mental operations needed for these tasks.

For the Go/no-go task, the biggest activation cluster was found in the right prefrontal cortex, which included the DLPFC and IFG (Nee et al., 2007). Further clusters were in the left DLPFC and ACC. In this task, overcoming the prepotent tendency to respond can be overcome in two ways. One is to bias processes to select the appropriate response, which can be described as attentional control. Participants may pay particular attention to specific stimulus features that facilitate discrimination. The other way would be to stop or inhibit an inappropriate response from being executed in no-go trials. The exact setup of the task is likely to influence the relative contribution of the two mental operations to task processing. The more go signals occur before a no-go signal, the bigger is the prepotent tendency to respond. Successful resolution of no-go trials might then depend on response inhibition to a larger degree. A few studies have systematically varied the amount of go trials before a no-go trial (Durston, Thomas, Worden, Yang, & Casey, 2002; Garavan, Ross, Murphy, Roche, & Stein, 2002). They found that activity in the right IFG was increased when the prepotent tendency to respond was stronger. Another study reported that an increase in the relative amount of no-go trials led to increased activity in the right prefrontal cortex, including the DLPFC (De Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000). These findings suggest that the (right) IFG is critically involved in inhibiting a predominant response, whereas the DLPFC is associated with more controlled style of information processing and response selection.

In the stop-signal task, the stop signal is delivered *after* the go signal. Thus participants have already initiated the process leading to a response, and must then stop it. Different from the go/no-go task, resolution of the conflict relies solely on motor response

inhibition. Consistent with the reasoning above, two fMRI studies of the stop-signal task have reported a predominant role of the right IFG for successful response inhibition (Rubia et al., 2001; Rubia, Smith, Brammer, & Taylor, 2003). Activation was also reported in the presupplementary motor areas (pre-SMA) and the ACC. Further evidence for a key role of the IFG in response inhibition stem from lesion studies. Different from neuroimaging, lesion studies can provide evidence what regions are absolutely necessary for cognitive functions. The size of lesions in the right IFG have been shown to correlate with response inhibition impairments in the stop-signal task (Aron, Robbins, & Poldrack, 2004). Another study recorded intracranial EEG in the right IFG while patients being evaluated for epilepsy performed the stop-signal task (Swann et al., 2009). A significantly greater IFG response was found for successful than unsuccessful stop trials.

The Flanker task mainly activated the right DLFPC and right insula. There was a significant overlap with activity elicited by the Go/no-go task. Both tasks require selective attention in order to bias processing against an inappropriate response. Compared to the other tasks, error rates are much lower for the Flanker task. This suggests that there might be less need to inhibit erroneous responses during execution. Correspondingly, the IFG was less activated in the Flanker task than in the other tasks.

The Stroop task, like the Flanker task, also requires filtering out irrelevant information. However, relevant and irrelevant information are features of the same stimulus. Also, reading is highly automated, contributing to the prepotency of the incorrect response. Error rates are considerably higher than in the Flanker task. This suggests that both selective attention and inhibition are important for correct Stroop task processing. Accordingly, activity in the Stroop was found in the ACC, the DLPFC bilaterally, and the left IFG. Clusters were much bigger in the left hemisphere (Nee et al., 2007), while the activity in right DLPFC overlapped with the one from Flanker task. The bilateral DLPFC

involvement might reflect the high demand of selective attention and response selection in the Stroop task. The left predominance is probably related to the strong verbal nature of the task.

The ACC was activated in all tasks but the Flanker task in the meta-analysis by Nee et al. (2007). Yet another review concluded that the ACC is also reliably activated in the Flanker task (Botvinick, Cohen, & Carter, 2004). A cognitive process necessary for all tasks studied in the field of cognitive control research is the detection of a conflict during information processing in the first place. The ACC and adjacent midfrontal areas are implicated in conflict detection and error monitoring (Botvinick et al., 2004; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Kerns et al., 2004; Van Veen & Carter, 2002). The ACC is thought to detect conflict between simultaneously active, competing mental representations and to alert systems involved in top-down control to resolve this conflict.

From a social-psychological point of view, inhibition might be what lies most at the heart of self-control. In accordance with the reasoning above, research on addiction has outlined a key role of the IFG for affective and nonaffective self-control. The size of the right IFG decreases with years of drug abuse (Ersche, Williams, Robbins, & Bullmore, 2013). Furthermore, the decrease in the IFG size correlates with impairments in the stop-signal task performance as well as emotion regulatory success and loss of control over craving in drug users (Tabibnia et al., 2011). Aron, Durston, et al. (2007) have laid out a more detailed theory how responses and interruption by the IFG come together in the human brain. At first, a go process is initiated by the premotor cortex, which activates the primary motor cortex via the basal ganglia. The primary motor cortex then sends the signal to the relevant muscles through the corticospinal tract. The stop process may interfere with the go process by inhibiting cortical motor activity via the pre-supplementary motor area, or by influencing activity in the basal ganglia through a subthalamic nucleus-globus

pallidus pathway. Crucially, both the subthalamic nucleus and the pre-SMA were found to be directly connected with the IFG via white matter tracts (Aron, Behrens, Smith, Frank, & Poldrack, 2007; Aron, Durston, et al., 2007). The work from Aron's group has specifically popularized the view of the right IFG as the critical area for inhibition. Both laterality and function are not without counter-proposals (e.g. Swick & Chatham, 2014). A lesion study (Swick, Ashley, & Turken, 2008) demonstrated that the left IFG is critical for inhibition as well. Others have argued that the right IFG's function is not specifically inhibition, but it is more generally involved in the detection of salient or task-relevant cues (Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010). Another meta-analysis focusing on Stop-signal and Go/no-go tasks found major common clusters in the anterior insula and the pre-supplementary motor area (pre-SMA), but not in the IFG (Swick, Ashley, & Turken, 2011). The pre-SMA lies within the medial prefrontal cortex, adjacent to the ACC as well as (pre)motor areas. Aron, Behrens, et al. (2007) suggested that the pre-SMA plays a role in detection and resolutions of conflicts which are specifically related to motor response inhibition. The anterior insula has been related to a wide range of conditions and behaviors, including awareness of bodily feelings (Craig, 2009) and conscious error perception (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010), but its role in inhibition task has received little attention. The insula lies in close proximity to both the DLPFC and IFG. Nee et al. (2007) found the insula to be generally activated by cognitive control tasks, but suggest that there is no conclusive evidence if the insula is implicated in response selection or response inhibition. However, Swick et al. (2011) argue that the pre-SMA is the actual area implementing motor inhibition, while the IFG and insula are involved in attentional control. Further research on the contributions of the pre-SMA, the IFG and insula to motor stopping is needed for clarification.

In sum, cognitive neuroscience has distinguished three mental operations which can be considered core-components of self-control: action/conflict/error monitoring, selective attention/attentional control/response selection, and response inhibition. With regard to anatomical regions, the most widespread view is that the ACC is important for conflict monitoring and error detection, the DLPFC for selective attention and response selection, and the IFG for inhibition, though there is some debate about the exact function of the lateral prefrontal areas (DLPFC, IFG).

1.5 Neuroscientific studies of self-control exertion

Only few neuroscientific studies have investigated self-control exertion effects. This chapter will describe all which implemented the dual-task design. According to the two-stage model of self-control, successful execution of self-control entails first the identification of a conflict (recognizing the need for control), and second conflict resolution (actual implementation of control; Myrseth & Fishbach, 2009). The first two studies examined which stage was affected by self-control exertion. In an electroencephalogram (EEG) study by Inzlicht and Gutsell (2007), participants either had to watch an emotional film naturally (control condition) or suppress their emotions (self-control exertion condition). Prior self-control exertion led to slower reaction times in the Stroop task. To analyze the EEG signal, the brain response to trials was averaged to form the even-related potential. Relative to the control condition, the self-control exertion condition revealed a weaker error-related negativity (ERN), a specific part of the event-related potential, after error commission. The ERN is associated with conflict monitoring and error detection (Gehring, Goss, & Coles, 1993). Research indicates the ERN originates from the dorsal anterior cingulate cortex and alerts top-down control to resolve conflicts and errors (Van

Veen & Carter, 2002). The findings from Inzlicht and Gutsell (2007) thus suggest that self-control exertion impairs the detection of conflict, the first stage of self-control.

Second, Hedgcock, Vohs, and Rao (2012) looked into the same question using fMRI. The first task was an attention-control task where participants looked at a fixation cross in the middle of the screen while words appeared periodically around the cross. In the self-control exertion condition, participants were told to ignore the words and not to read them. In the control condition, they were told that the words could be looked at or ignored. The second task was a choice task, where participants read a scenario description first and then had to indicate their preference from a list of options (e.g. choose among different college courses). Behaviorally, prior self-control exertion led to faster decisions in the choice task. Neurally, self-control exertion decreased activity in the right middle frontal gyrus during the choice task, but no changes were detected in the ACC. These findings contradict the ones from Inzlicht and Gutsell (2007) and suggest that self-control exertion impairs the implementation stage of self-control.

The third neuroscientific study examined effects of emotion regulation on cognitive performance (Friese et al., 2013). Participants saw emotionally negative pictures and had to either suppress their emotions (self-control exertion condition) or leave them unchanged (control condition). Subsequently they engaged in a Stroop task. Participants in the self-control exertion condition showed stronger Stroop interference effects than participants in the control group. The authors found that participants in the self-control exertion condition activated the right middle and inferior frontal gyrus more during the picture-viewing task, but less in the subsequent Stroop task, than participants in the control condition. In addition, Friese et al. (2013) specifically tested for potential changes in ACC functioning induced by self-control exertion, but found no differences. This again

supports the view that depletion affects self-control implementation. Despite these differences, these studies adequately demonstrate how self-control exertion effects can be integrated into a general framework of structures related to cognitive control.

Fourth, the fMRI study by Persson et al. (2013) is the first to report brain activity during both the first and the second task. In the first task, in each trial a set of four letters appeared on screen and subsequently a target letter. Participants had to indicate if the target letter had been presented before as part of the four-letter set. In the control condition, all negative targets were nonrecent, meaning that the letter had not appeared in the current set or the last two presented sets. In the depletion condition, two thirds of negative targets were not members of the current set, but were presented as part of the two immediately preceding sets. The second task was a verb generation task where a noun was presented and participants had to generate a related verb. The nouns had either many associated verbs (e.g., ball: throw, kick, bounce, etc.) or few to one associated verb (e.g. scissors: cut). Nouns with many associations demanded interference control and participants exhibited longer reaction times on these than nouns with few associations. Reaction times for nouns with many associations were increased even further for participants in the depletion condition. Brain activity in the depletion condition during the second task was reduced in the left IFG, ACC, striatum and cerebellum, as compared to the control condition. Interestingly, depletion increased activity at contralateral sites; namely the right inferior frontal gyrus/anterior insula, superior temporal gyrus, and the posterior insula. A conjunction analysis showed that (part of) the left IFG was activated by both tasks. Lastly, the amount of activity decrease in the left IFG (compared to a pre-depletion verb generation task) correlated with the magnitude of the behavioral depletion effect. The tasks have only been used once in another study which was conducted by the same group (Persson, Welsh, Jonides, & Reuter-Lorenz, 2007). Instead of referring to

self-control exertion, the authors explain their findings in the context of process-specific fatigue, namely interference resolution. Nevertheless, control of interference as demanded by these tasks can also be described as inhibition and fits within the self-control literature. In sum, this paper provided further evidence that depletion decreases activity in areas involved in cognitive control. It is the first study which reported that increased activity in prefrontal control areas (IFG) during the first, depletion-inducing task overlapped with subsequent activity decreases during the second task. Furthermore, it is the only study which reported increased activity after depletion.

Fifth, Wagner and Heatherton (2013) examined the effects of self-control exertion on emotional processing. As a first task, participants watched a documentary film while a sequence of unrelated words appeared randomly on screen. Participants in the depletion condition were told to inhibit reading the words, while control participants were told they could decide freely whether to read the words or not. The second task consisted of watching emotionally negative, neutral, and positive words while making indoor/outdoor judgements. Participants were not instructed how to watch the emotional pictures, but it was assumed they would engage in spontaneous emotion regulation (see manuscript 3 for a more detailed discussion). Following self-control exertion, activity in the amygdala was increased, especially for emotionally negative pictures. While the authors did not report depletion-induced prefrontal activity decreases, they found that connectivity between the amygdala and the VMPFC was decreased after self-control exertion. This area has been implicated in emotion suppression (e.g. Urry et al., 2006), though its function is not without controversies (Buhle et al., 2014; Diekhof, Geier, Falkai, & Gruber, 2011).

Sixth, Wagner et al. (2013) investigated in another fMRI study depletion effects in dieters. As in this group's previous study, participant first watched a film while they either had to inhibit reading words (depletion condition), which appeared randomly on screen,

or could decide freely to read them or not (control condition). Subsequently participants saw pictures of highly liked and craved food items, mixed with control items. Participants had to indicate whether the picture showed an indoor or outdoor scene. While viewing food items, depleted participants activated the left orbitofrontal cortex more strongly than control participants. The area is considered to encode the emotional valence or subjective reward of stimuli (Demos, Heatherton, & Kelley, 2012; Ochsner, Silvers, & Buhle, 2012; Van Der Laan, De Ridder, Viergever, & Smeets, 2011). The ventral striatum/nucleus accumbens, although an a priori ROI, showed no significant difference between the conditions. Yet depletion led to reduced connectivity between the IFG bilaterally and the OFC, and between the IFG bilaterally and the ventral striatum. A critical remark about their statistical procedure must be added. In a first step, they identified ROIs by comparing food versus control trials with a cluster-level threshold of $p < .05$. In a second step, they performed *t*-tests for effects of depletion on activity extracted from these ROIs. For areas involved in representing the emotional value of food, i.e. the OFC and ventral striatum, an uncorrected threshold of $p < .05$ was employed. This procedure is almost identical to looking at fMRI results at $p < .05$, uncorrected, which is unusual because of a high probability of false-positives. The effect in the left OFC reached significance under these circumstances, but was not very strong, $t(29) = 2.20$, $p = .036$ (uncorrected). This raises questions about the reliability of their findings.

Seventh and last, Wang, Yang, and Wang (2014) examined how different emotion regulation strategies relate to self-control exertion. This EEG study built upon the findings from Inzlicht and Gutsell (2007), which reported a decreased error-related negativity (ERN) after emotion suppression. Participants watched a sad movie and were instructed to suppress their internal and facial reactions (emotion suppression group), adopt a neutral and objective attitude towards the movie (reappraisal group), or watch it carefully

(control condition group). EEG was recorded during a subsequent Stroop task. The reappraisal group, but not the emotion suppression group, indicated to have successfully reduced their sad emotions, relative to the control group. Compared to the control and the reappraisal group, participants who suppressed their emotional response committed more errors in the Stroop task. The suppression group also had a weaker ERN after errors than the other two groups. Later components of the event-related potential (ERP), such as the post-error positivity or the N450, showed no significant effects. Taken together, only emotion suppression seems to induce self-control exertion. Reappraisal is not only a more effective, the dual-task paradigm confirms it is also less effortful than suppression.

In summary, there is a rising interest in examining the neural underpinnings of self-control exertion. While two EEG studes have reported depletion-induced changes in error monitoring (Wang et al., 2014), only one fMRI study found corresponding activity reductions in the ACC (Persson et al., 2013). All fMRI studies instead reported depletion-induced changes in prefrontal functioning, either related to activity, or connectivity. Furthermore, there is first neuroscientific evidence for increased emotions and desires after depletion, probably due to decreased influence from regulatory areas (Wagner et al., 2013; Wagner & Heatherton, 2013).

1.6 Emotion regulation

Emotion regulation refers to processes which influence which emotions we have, when we have them, and how we experience and express them (Gross, 2002). Similar to other domains of self-control, emotion regulation is a means to override the innate tendency how to react to a given situation. In fact, emotion regulation is frequently used to induce states of depletion (e.g. Friese et al., 2013; Muraven et al., 1998; Wagner &

Heatherton, 2013). This chapter will provide an overview of emotion regulation strategies, and brain areas critical for generating and regulating emotions.

There is a potentially limitless number of emotion regulation strategies. The highly influential process model of emotion regulation (which has nothing to do with the process model of self-control) groups emotion regulation strategies into families based on a stimulus-organism-response time line (Gross, 2002). Emotion regulation families differ in when they have their primary impact on the emotion-generative process, as detailed in Fig. 2. First, situation selection refers to approaching or avoiding situation which are likely to cause desirable or undesirable emotions. For example, you may choose not to go near a person you do not like. Second, individuals may modify a situation. For example, if you're newly divorced and are asked about your partner, you may choose not to talk about it. Third, instead of changing a situation, individuals may direct their attention in order to influence their emotions. For example, if you are watching a horror movie where some scenes are too intense, you may distract yourself by counting the people watching the film. Fourth, individuals may make a cognitive effort to change how a situation is appraised. Reappraisal in particular involves changing the way we think about an emotional stimulus in order to alter its emotional impact. For example, when watching a horror movie, you may tell yourself that persons in the film are actors and nobody got hurt. Fifth and finally, response modulation refers to alter physiological, experiential, or behavioral effects as directly as possible after an emotion has already been elicited. This often involves suppressing facial reactions. For example, you may wish to hide your shame about not watching the whole horror movie from your friends (Gross & Thompson, 2007; Gross, 2002).

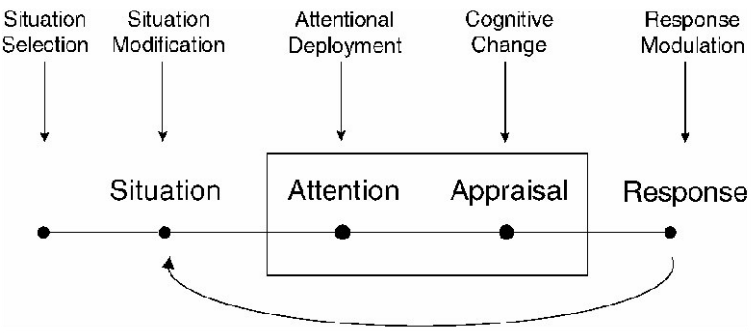

Fig. 2. The process model of emotion regulation which highlights five families of emotion regulation strategies. The rectangle represents the "black box", i.e. what is happening inside the person. The feedback arrow indicates that an emotional response often changes the situation that gave rise to the response in the first place. Retrieved from "Emotion regulation: Conceptual foundations" by J. J. Gross & R. A. Thompson, 2007, p. 10, in J. J. Gross (Ed.), Handbook of Emotion Regulation (pp. 3–24), New York, NY: Guilford Press.

Several brain areas are involved in emotion generation (Ochsner et al., 2012). The amygdala is implicated in encoding all emotionally relevant stimuli. It reacts strongly to arousing stimuli and is very sensitive to potential threat cues, such as expressions of fear. The ventral striatum/nucleus accumbens is involved in learning which cues predict reward or reinforcement. The ventromedial prefrontal cortex (VMPFC), sometimes used synonymously with the orbitofrontal cortex, evaluates input from the amygdala and ventral striatum as well as various other regions such as the temporal lobe (memory) or prefrontal cortex (cognitive control) with respect to current goals. The VMPFC is thought to be important for decision making. Finally, the anterior insula is implicated in bodily sensations which can have a strong affective component (e.g. disgust), and in negative affective experience in general.

Four meta-analyses on the neural correlates of emotion regulation have been conducted in the last years (Buhle et al., 2014; Diekhof et al., 2011; Frank et al., 2014; Kohn

et al., 2014). While these analyses differed in the number of studies included and in the criteria for study selection, these differences seemed to have negligible effects on the results. In concert, they found that decrease in amygdala activity was the primary or only effect of successful emotion regulation. Activity increases were consistently reported in the IFG and middle frontal gyrus (MFG) bilaterally, ACC, and left middle temporal cortex. In addition, some of the meta-analyses reported uni- or bilateral clusters in the superior frontal gyrus (Buhle et al., 2014; Diekhof et al., 2011; Frank et al., 2014), the pre-SMA and SMA (Frank et al., 2014; Kohn et al., 2014), the medial frontal gyrus (Buhle et al., 2014; Diekhof et al., 2011), and parts of the parietal cortex (Buhle et al., 2014; Kohn et al., 2014). Parts of areas involved in emotion generation have also been found to increase activity when regulating emotions, namely the VMPF (Diekhof et al., 2011) and the anterior insula (Diekhof et al., 2011; Kohn et al., 2014).

Instead of areas specific to emotion regulation, it seems that prefrontal and cingulate systems that support cognitive control are also main hubs for emotion regulation. The DLPFC, that is the middle and superior frontal gyrus, may direct attention to features of stimuli relevant for the regulatory process. It may even support manipulation of appraisal in working memory (Buhle et al., 2014). The ACC may monitor the extent to which the regulatory process changes the emotional response in the intended way. The IFG may inhibit processing of features which would strengthen the emotional response in the undesired way. Different from other prefrontal structures, the IFG has direct anatomical connections with the amygdala (Kohn et al., 2014). On the one hand, a lot of literature on emotion regulation has addressed the IFG (or VLPFC) as a core regulatory center. On the other hand, similar to the debate of the IFG's role in cognitive control, the precise contribution of the IFG to emotion regulation has been questioned. Specifically, Kohn et al. (2014) argue that the IFG may rather be involved in the perception of emotions and signal

the need to regulate to other brain areas. Buhle et al. (2014) offered a potential explanation for the consistent additional involvement of the left middle temporal cortex. They suggested that prefrontal and parietal control areas influence the lateral temporal areas, which are associated with semantic and perceptual representations. Consistently, it has been suggested that reappraisal works by altering the semantic and perceptual representations of stimuli in such ways that change their emotional significance. For example, when watching a horror movie, you may tell yourself that "it's just a movie, not real".

Diekhof et al. (2011) presented slightly different findings and a different interpretation. They found overlapping activity in the VMPFC, and a predominant role in controlling negative affect by cognitive emotion regulation strategies such as reappraisal. This assumption is supported by the finding that anatomical connections between lateral prefrontal regions and the amygdala are relatively sparse, but there are many connections from lateral prefrontal areas to the VMPFC, and from the VMPFC to the amygdala. Thus the VMPFC could take a mediating role between regulating and emotion-inducing areas. However, the other meta-analyses did not support this view since they failed to find activity in the VMPFC (Buhle et al., 2014; Frank et al., 2014; Kohn et al., 2014).

1.7 Research questions

Social-psychological research has provided evidence for depletion effects across various tasks. Yet very little is known about the mechanisms which underlie this effect, and it is an open question if self-control draws on a limited resource. The first neuroscientific studies on self-control exertion have emerged, but so far present a very diverse picture of the brain areas and mental processes influenced by self-control exertion. However, fMRI studies provide an additional, neural layer to examine depletion which has

could fundamentally contribute to our understanding of the causes, mechanisms, effects, and neurophysiological understanding of depletion effects.

The first study relates to the ongoing debate between resource and motivational models to explain depletion effects. As I have outlined in the introduction, findings of reversing depletion effects by motivation have been interpreted both to support the strength model or motivational models. So far, behavioral studies have been unable to provide deciding evidence for one model or the other. Measuring concurrent brain activity might help to differentiate between effects of depletion and motivation on the brain, or, alternatively, show that they are indeed indistinguishable.

In the second study, we examined the effects of self-control exertion on the human brain during a subsequent period of rest. Measuring functional connectivity in the resting state has been increasingly popular in recent years. This approach provides a unique opportunity to assess self-control exertion effects in the absence of further task engagement. In addition, we opted for an emotion suppression task to induce self-control exertion.

The third study was intended to investigate links between depletion, emotional processing, and emotional memory formation. Several studies suggest that depletion strengthens emotional experiences. From memory research, it is known that emotional experiences are better than neutral ones. While nobody has examined this hypothesis before us, it seems reasonable to assume that individuals will remember emotional events better if they are experienced in a state of self-control exertion.

2 Manuscripts

2.1 First study: Motivational incentives lead to an over-increase in lateral prefrontal activity after self-control exertion

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2.2 Second study: Altered brain connectivity in the resting state fMRI after self-control exertion

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Second study: Altered brain connectivity in the resting state fMRI after self-control exertion

Abstract

Emotion suppression requires costly regulatory efforts, and can lead to subsequent decrements in other self-control demands. Such performance drops have become known as depletion effects. Yet, the neural mechanisms underlying these effects remain largely unclear. Resting state functional magnetic resonance imaging (fMRI) is a way to describe connectivity and neural functioning at rest and might reveal new insights into the neural underpinnings of depletion effects. In a within-subject design, participants engaged in a picture task twice, in which they either had to suppress their emotional responses (depletion condition) or leave the emotional responses unaltered (watch condition). Rest state connectivity was measured before and after each task. Emotion suppression led to increased connectivity during rest in areas critically involved in emotion regulation, namely between the inferior frontal gyrus and the middle temporal gyrus. In addition, this connectivity difference correlated with subjective exhaustion. By contrast, watching emotional pictures decreased connectivity between areas associated with task engagement and rest. These results suggest that sustained task connectivity might contribute to depletion effects by rendering it more difficult for these areas to establish close connections to other brain areas that may be important for subsequent self-control tasks.

Keywords: Emotion regulation, resting state, fMRI, suppression, self-control, depletion

Introduction

In everyday life, individuals make use of a variety of ways to regulate their emotions, one of them being the suppression of emotional responses and their expression. Emotion suppression is effortful and costly (Gross, 2002; Richards, 2004), and might even

take a toll on subsequent regulatory actions (Binder et al., 2012; Wang et al., 2014). Regulatory limits have been studied extensively in behavioral research on self-control. When individuals engage in regulatory actions, be it emotion suppression or other forms of self-control, subsequent performance temporarily drops. This observation has become known as depletion effects (Baumeister & Heatherton, 1996; Baumeister et al., 2007; Hagger et al., 2010). Yet, the causes and mechanisms behind depletion effects remain poorly understood and are subject to an ongoing debate (Baumeister, 2014; Inzlicht et al., 2014; Kool & Botvinick, 2014; Kurzban et al., 2013). Behavioral studies have relied on measuring the detrimental effect of prior self-control exertion on subsequent tasks. This is a rather indirect way to assess self-control exertion. Advances in functional magnetic resonance imaging (fMRI) have made it possible to examine brain functionality in the absence of task engagement, potentially providing a new perspective on self-control exertion.

Over the last decade, a growing interest has emerged in investigating the human brain in the resting state (RS). Neural processing is characterized by spontaneous low-frequency signal fluctuations, which show relatively stable signal correlations over wide areas of the brain and are organized into distinct functional connectivity networks (De Luca, Beckmann, De Stefano, Matthews, & Smith, 2006). These networks have been linked to the intrinsic functional architecture of the brain (Smith et al., 2009) and can be detected with functional magnetic resonance imaging (fMRI). One of the most prominent connectivity networks is the default mode network (DMN), which encompasses midline structures such as the medial prefrontal cortex and the ventral anterior and posterior cingulate cortex. The DMN can reliably be measured during various mental states, and it partly persists even during sleep (Fukunaga et al., 2006; Sämann et al., 2011). Despite this stability, DMN connectivity also varies over time and as a function of several contextual factors. For example, evidence suggests that DMN connectivity alterations are related to internally

driven cognitive processes such as self-related thoughts and mind wandering (M. D. Fox et al., 2005; Mason et al., 2007; Raichle & Snyder, 2007). It has also been shown that connectivity strength within and between connectivity networks varies as a function of task engagement (M. D. Fox et al., 2005; Smith et al., 2009). Activity in the DMN is suppressed when participants focus attention on external stimuli, e.g. during task engagement, and instead connectivity in the so-called task-positive network (TPN) is increased, typically encompassing the dorsolateral prefrontal cortex, the inferior frontal gyrus, the posterior parietal cortex, and further task-specific areas (M. D. Fox et al., 2005).

There is evidence that previous activities can be reflected in subsequent resting state connectivity. Studies have shown that increased connectivity in the TPN during periods of rest after task engagement is related to learning and memory consolidation (Albert, Robertson, & Miall, 2009; Stevens, Buckner, & Schacter, 2010). Others have examined the effects of effortful cognitive task processing on subsequent resting states, and reported varying findings (Esposito, Otto, Zijlstra, & Goebel, 2014; Evers, Klaassen, Rombouts, Backes, & Jolles, 2012; Pyka et al., 2009). For the DMN, either increased connectivity (Esposito et al., 2014; Pyka et al., 2009) or no effect (Evers et al., 2012) was reported. For the TPN, increases (Evers et al., 2012), decreases (Esposito et al., 2014) or no effects on connectivity (Pyka et al., 2009) have been found. Though all studies aimed at measuring effects of mental exhaustion in the subsequent RS, comparability of results is hampered by widely different study designs, which ranged from very short cognitive task engagement of less than a minute (Pyka et al., 2009), over sustained performance of various cognitive tasks for one and a half hours (Evers et al., 2012), to training and practice with a flight simulator for four hours (Esposito et al., 2014).

The present study aimed at examining RS connectivity alterations with fMRI after self-control exertion. Emotion suppression was chosen as the task to induce self-control

exertion and task duration was chosen in accordance with self-control research on depletion effects. In light of the inconsistent findings of connectivity alterations after prior task engagement, we opted for examining changes in both the TPN and DMN. Emotion regulation and cognitive control have been shown to rely on the same prefrontal brain areas, including the middle and inferior frontal gyrus (Buhle et al., 2014; Kohn et al., 2014; Ochsner et al., 2012). The inferior frontal gyrus (IFG) is considered to be a core structure for self-control (Aron, 2007; Tabibnia et al., 2011) and it has been associated with depletion effects in a number of self-control studies (Friese et al., 2013; Persson et al., 2013; Wagner et al., 2013). We decided to focus on the IFG to examine the TPN and used activity during the emotion suppression task to functionally localize the seed area for the RS analysis. Regarding the DMN, frequently used seed areas are the medial prefrontal cortex and the posterior cingulate cortex (PCC). Ventral parts of the medial prefrontal cortex have also been reported to be involved in emotion regulation and depletion effects, which lies in close proximity and is partly overlapping with medial prefrontal areas associated with the DMN. Thus for a better interpretability of outcomes we chose the PCC as seed area for the DMN.

Methods

Participants

According to Carter and McCullough (2013), the overall depletion effect corrected for publication bias is medium, $g = 0.48$ (trim-and-fill correction method). G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) indicates that to achieve 80% power in a within-subject design, 29 participants are sufficient. We measured 29 participants, but had to exclude one due excessive movement during the scanning periods. The remaining 28 participants

consisted of 5 males and 23 females and were on average 24.32 years old (*SD* = 3.52). Written informed consent was obtained from all participants and they received CHF 25/hour (approximately U.S. $26). The local ethics committee approved the study.

Procedure

In a within-subject design, participants engaged in two fMRI scan sessions. In one session, they suppressed emotions while watching neutral and negative pictures (suppress condition). In the other session, participants simply watched neutral and negative pictures (watch condition). Specifically, each scan session consisted of an anatomical scan, a pre RS scan, the picture task, and a post RS scan. Between the two sessions, participants had a break of at least 40 min, during which they could rest on a couch, listen to relaxing music, or read magazines. The order of the conditions (suppress, watch) was counterbalanced across participants. An overview of the study procedure is provided in Fig. 1. After scanning, participants filled out questionnaires including control questions, a manipulation check, and demographic data. Participants were then debriefed and thanked.

Manipulation Check

Following standard procedures in the behavioral literature on depletion effects, participants answered four questions (7-point Likert scale) after each scan session about how strenuous the task was, how much concentration it demanded, how much they had to control themselves, and how difficult the task was. A subjective exhaustion score was calculated by summing all four items (Cronbach's $\alpha = .65$). As expected, the emotion suppression condition was rated as more exhausting than the watch condition, suggesting that the manipulation of self-control exertion during the picture task was successful ($t(27) = 7.08$, $p < .001$).

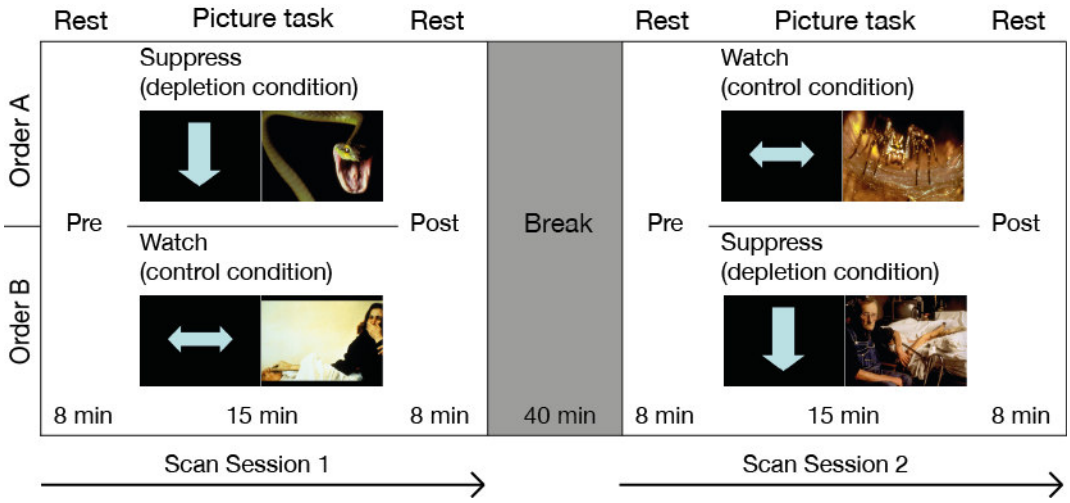

Fig. 1. Study Procedure. Participants engaged in two fMRI scan sessions, once in the depletion condition, once in the control or watch condition.

Picture Task

In each picture task, participants were exposed to 24 negative and 24 neutral pictures, grouped to blocks of four pictures of the same valence. Each block started with a short instruction (6 s) to either suppress the emotions elicited by the pictures (negative blocks in the suppress condition) or to simply watch the pictures (negative blocks in the watch condition and neutral blocks in both conditions). Pictures were presented for 6 s each. After each picture, participants rated their arousal on a four-point Likert scale (1 = calm, 4 = aroused) with a response pad, and saw a short reminder of the current instruction (downward arrow for suppress, horizontal arrow for watch). Time between pictures was 8 s. The two sets of 48 pictures each (24 negative and 24 neutral pictures) were taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008). The order in which the two sets of pictures were presented was counterbalanced across participants and with respect to condition order.

Prior to scanning, participants received a detailed written instruction. For the suppress condition, they were instructed to suppress any emotional reactions to the negative

pictures. They were told to try to stay calm inside and outside. They were instructed to imagine a protective shield from which emotions bounce off and to show no facial reactions, as if keeping a poker face. Furthermore, participants were told that a camera would film their faces during picture viewing and that observers should not be able to tell their emotional reactions based on these recordings. Even though we did not have a camera in the scanner, none of participants subsequently expressed any doubts about the supposed recordings. For the watch condition, participants were instructed to leave the emotional reactions as natural as possible, without changing them intentionally. Task design follows previous depletion studies where emotion suppression was used to induce self-control exertion (Baumeister et al., 1998; Friese et al., 2013).

Functional imaging

MRI scanning was performed on a Philips Intera 3 T whole-body MR unit at the University Hospital of Zurich, Switzerland. Functional time series were acquired with a sensitivity encoded, single-shot echo-planar sequence (SENSE-sshEPI) sensitive to BOLD contrast (T2* fast field echo with the following acquisition parameters: TR (repetition time) = 2500 ms, TE (echo time) = 35 ms, FOV (field of view) = 0.22 cm, acquisition matrix = 80 x 80, interpolated to 128 x 128, voxel size: 2.75 x 2.75 x 3.30 mm^3, no gap and SENSE acceleration factor R = 2.0). By using a midsagittal scout image, 40 contiguous axial slices were placed to the anterior–posterior commissure plane covering the entire brain.

Data analysis

MATLAB Release R2015a and SPM12 (www.fil.ion.ucl.ac.uk) were used to analyze the fMRI data. In addition, the functional connectivity toolbox CONN 15.e (Whitfield-Gabrieli & Nieto-Castanon, 2012) was used for RS analyses. The same preprocessing steps in SPM12 were applied to RS and task-based fMRI data. Images were realigned to correct

for head movement and corrected for differences in acquisition time between slices. Participants' individual T1-weighted structural image was co-registered with the mean functional image, segmented into gray matter, white matter, and cerebrospinal fluid tissue, and normalized to the standard T1 MNI template. Functional images were normalized to the standard MNI template using the transformation matrix from the T1 normalization procedure and spatially resampled to 2x2x2 mm voxels. Artifact Detection Tools (ART; Whitfield-Gabrieli & Nieto-Castanon, 2012) were used to identify movement or other outlier images in the fMRI time series based on a liberal threshold (above 99 percentile). Finally, images were spatially smoothed using an 8 mm FWHM Gaussian kernel.

Picture task. A 128-sec-cutoff high-pass filter was added to the confound partition of the design matrix to account for low-frequency drifts, and a correction for intrinsic autocorrelations was included in the analysis. For every subject, a GLM was set up with three regressors of interest (negative pictures, neutral pictures, button presses indicating arousal), which were convolved with a canonical hemodynamic response function (HRF), and six movement parameters derived from realignment correction as regressors of no interest. If ART detected outlier images, they were deweighted in the GLM with additional regressors. Contrast images for each participant were obtained by subtracting neutral images from negative images. To identify areas associated with emotion suppression, group-level *t*-tests were performed by comparing suppression scan sessions with watch scan sessions. Based on converging involvement of the inferior frontal gyrus (IFG) in depletion effects and emotion regulation, we were particularly interested in activity in this area. The picture task was used to localize the IFG seed for the RS analysis. To this end, a 6 mm sphere was drawn around the IFG peak activity (MNI coordinates 48, 44, -10) in the emotion suppression contrast.

Resting state analysis. First, functional images were band-pass filtered (0.008 to 0.09 Hz) and the anatomical component-based noise correction method (aCompCor; Behzadi, Restom, Liau, & Liu, 2007) was applied to remove physiological and movement confounds. Specifically, aCompCor derived principal components from white matter and cerebrospinal fluid masks, which were included in a general linear model together with movement parameters and potential additional outlier regressors from ART, to remove artifacts from the functional image time-series. This approach has been shown to perform more effectively than other approaches, such as the more common global signal regression (Behzadi et al., 2007; Chai, Castañán, Öngür, & Whitfield-Gabrieli, 2012; Muschelli et al., 2014). Furthermore, for aCompCor, negative correlations have been shown to be valid indicators of functional RS connectivity (Chai et al., 2012). Bivariate correlation analyses were performed between seed regions and all other voxels in the brain in order to compare differences between post-suppress RS and post-watch RS. Fisher's *z*-transformation was applied to correlation values in order to statistically compare connectivity values between conditions. As a first seed region, the IFG ROI identified in the picture task was used to examine connectivity changes in the TPN. A 6 mm sphere centered on the posterior cingulate cortex (MNI coordinates 1, -55, 17) was used as a second seed region to examine connectivity changes in the DMN. To correct for multiple comparisons, family-wise error rate (FWE) correction was applied at the cluster level ($p < .05$) to voxels surviving an initial peak-level threshold ($p < .001$, uncorrected). In a next step, the first eigenvariate was extracted from regions showing connectivity changes in the post-task RS and compared with connectivity in the pre-task RS. On the one hand, tests for connectivity differences between conditions in the pre-task "baseline" were applied. On the other hand, pre-task and post-task connectivity was compared to examine if differences between conditions stemmed from increased or decreased RS connectivity. Finally, it was examined how RS

connectivity and task activity was related to subjectively reported exhaustion, using correlation and multiple linear regression analyses.

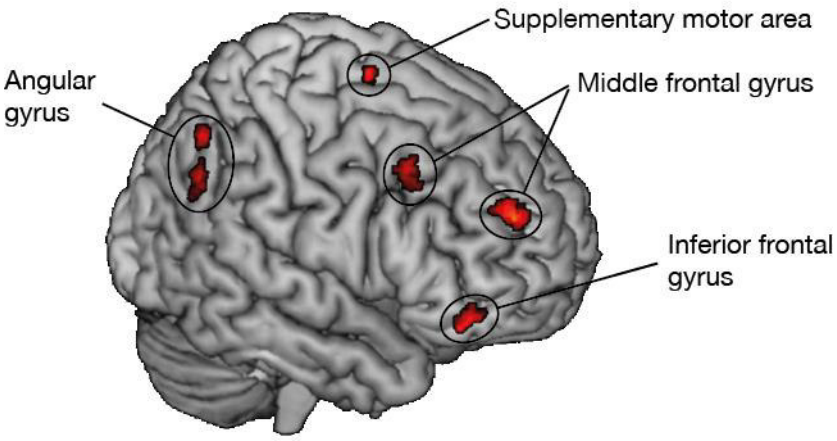

Fig. 2. Activity related to emotion suppression. Surface results are projected onto a canonical normalized T1 image. Not depicted are subcortical areas, such as the middle cingulate cortex, cuneus, and the caudate nucleus.

Results

Picture task

A comparison of the suppress condition with the watch condition showed activity in the middle cingulate cortex and the right angular gyrus when FWE rate correction was applied at the cluster level. These areas are typically involved in emotion regulation. Meta-analyses also point to a pivotal role of the IFG in emotion regulation (Buhle et al., 2014; Diekhof et al., 2011; Frank et al., 2014; Kohn et al., 2014). Since we were particularly interested in studying the IFG's role in depletion effects, we opted for a more liberal threshold of $p < .001$, uncorrected, which revealed activation in the right IFG, along with six further activity clusters, see Table 1 and Fig. 2. Peak coordinates of the right IFG activity (48 42 -12) were used as the center for an IFG seed area used in the RS analyses.

Table 1

Brain areas which were more strongly activated during the emotion suppression than the watch condition.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Middle cingulate cortex	159	23	R	8	-30	24	4.31
Angular gyrus	151	39	R	38	-48	30	3.91
Middle frontal gyrus	63	46	R	24	54	24	3.82
Cuneus	54	40	R	26	-52	34	3.72
Inferior frontal gyrus	30	47	R	48	42	-12	3.61
Supplementary motor area	11	6	R	18	-4	72	3.60
Middle frontal gyrus	34	44	R	42	22	36	3.44
Supplementary motor area	15	6	R	6	-6	66	3.44
Caudate nucleus	34		L	-12	-16	20	3.38

Note. Based on the contrast negative versus neutral pictures, this table reports clusters of stronger activity during the emotion suppression condition than during the watch condition, thresholded at $p < .001$ (uncorrected) in a minimum of five adjacent voxels. BA, Brodmann area; R, right hemisphere; L, left hemisphere.

Resting state

Task-positive network. To examine changes in the TPN, RS connectivity with the right IFG seed after the emotion suppression condition was compared to after the watch condition. Three clusters correlated more strongly with the IFG after emotion suppression. Two clusters were in the posterior part of the left middle temporal gyrus (MTG), which is an area typically reported in emotion regulation studies. The third cluster was in the rostral part of the orbitofrontal cortex (OFC) bilaterally (Table 2).

Table 2

Connectivity changes in the task-positive network and the default mode network.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*P*(FWE)
Stronger connectivity in the TPN (IFG seed) after emotion suppression							
Middle temporal gyrus	169	21	L	-62	-40	0	.002
Middle temporal gyrus	158	20	L	-46	-22	-14	.003
Orbitofrontal cortex	98	11	L&R	-8	66	-20	.037
Weaker connectivity in the TPN (IFG seed) after emotion suppression							
No suprathreshold clusters							
Stronger connectivity in the DMN (PCC seed) after emotion suppression							
Fusiform gyrus/inferior occipital cortex	249	19	L	-32	-80	-10	<.001
Inferior occipital cortex/ fusiform gyrus	192	37	R	50	-68	-14	.001
Weaker connectivity in the DMN (PCC seed) after emotion suppression							
Brainstem	194		L&R	8	-24	-34	.001

Note. Comparison of connectivity after the emotion suppression condition versus after the watch condition, thresholded at $p < .05$ (FWE rate corrected at the cluster level) after an initial peak threshold of $p < .001$ (uncorrected). BA, Brodmann area; R, right hemisphere; L, left hemisphere.

For further analyses, the two clusters in the left MTG were combined to one area, though the outcomes were very similar when analyses were performed on both MTG clusters separately. Connectivity between these areas did not differ in the pre-task resting states ($p > .35$ for both MTG and OFC), hence the differences did not stem from inconsistent pre-task baselines. Next the post-task resting states were compared with the associated pre-task resting states. For the left MTG, emotion suppression led to an increase

in connectivity ($t(27) = 2.41$, $p = .023$), and the watch condition led to a marginally significant decrease in connectivity ($t(27) = -1.94$, $p = .063$). For the OFC, there was only a tendency to increased connectivity in the emotion suppression condition ($t(27) = 1.89$, $p = .070$), but a significant connectivity decrease in the watch condition ($t(27) = -2.23$, $p = .034$). In sum, emotion suppression led to a subsequent increase in the TPN, whereas simply watching emotional pictures led to decreased connectivity between TPN areas as compared to baseline conditions. See Figure 3 for an overview of the results related to the TPN.

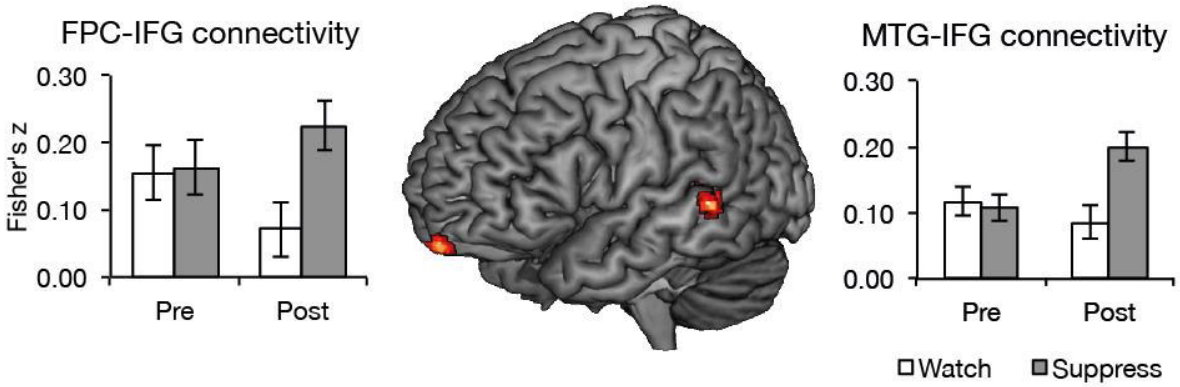

Fig. 3. Connectivity changes in the task-positive network. The orbitofrontal cortex (OFC) and the left middle temporal gyrus (MTG) showed connectivity differences with the inferior frontal gyrus (IFG) seed between the emotion suppression condition and the watch condition. Results are superimposed on a canonical normalized T1 image. Error bars indicate standard errors of the mean.

Default mode network. The same analyses as for the TPN were conducted with a PCC seed area. After the emotion suppression condition as compared to after the watch condition, connectivity with the PCC was stronger in two areas located in the left and right inferior occipital cortex (IOC), which included parts of the fusiform gyrus. For completeness, we report that connectivity with the PCC was weaker after emotion suppression in

a brainstem area (see Table 2). However, we will restrict further analyses to cerebral areas. Comparison of pre-task RS revealed no differences in baseline IOC-PCC connectivity values bilaterally (both *p*s > .5). Interestingly, post-task differences seemed to be primarily driven by a connectivity decrease in the watch condition (left IOC: $t(27) = -3.44$, $p = .002$; right IOC: $t(27) = -4.03$, $p < .001$), where the connectivity changed from a slightly positive to a slightly negative correlation. The connectivity increase after the emotion suppression condition was nonsignificant (left IOC: $t(27) = 1.23$, $p = .23$; right IOC: $t(27) = 1.63$, $p = .12$). See Figure 4 for an overview of the results related to the DMN.

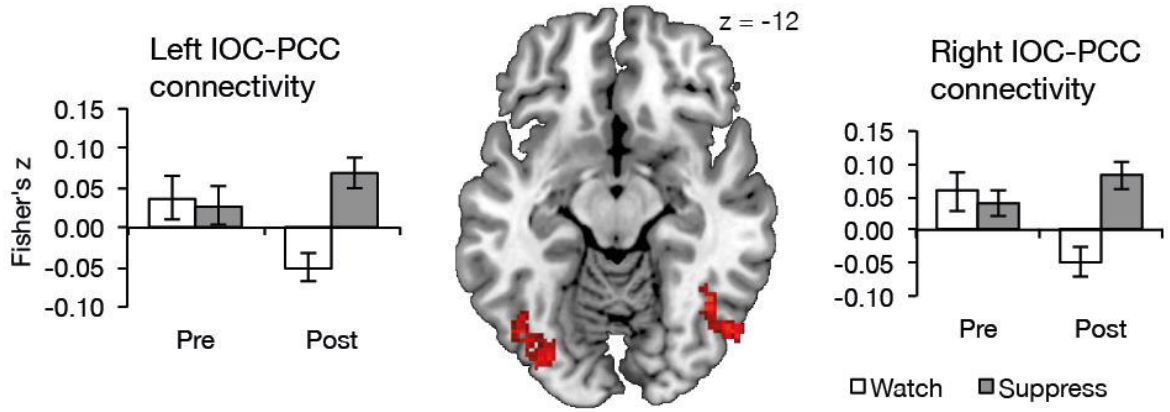

Fig. 4. Connectivity changes in the default mode network. The left and right inferior occipital cortex (IOC)/fusiform gyri showed connectivity differences with the posterior cingulate cortex (PCC) seed between the emotion suppression condition and the watch condition. Results are superimposed on a canonical normalized T1 image. Error bars indicate standard errors of the mean.

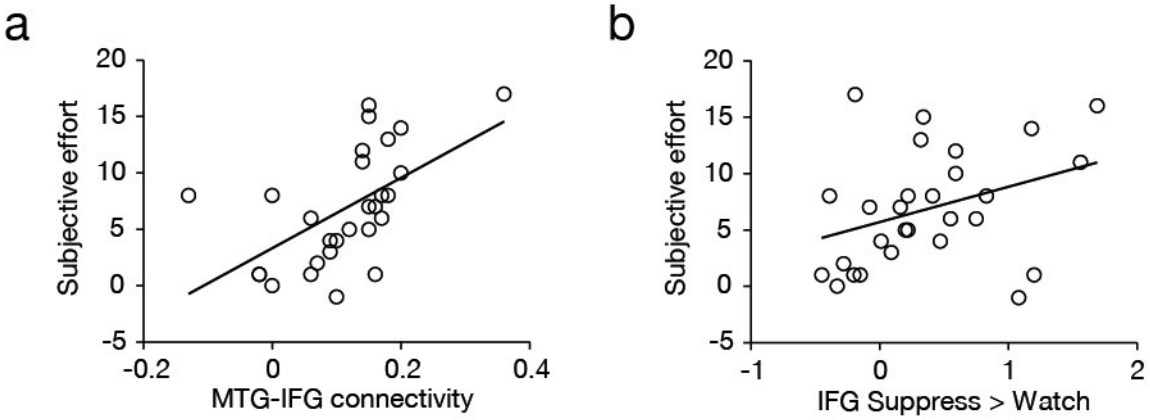

Fig. 5. Correlations of subjective exhaustion with brain connectivity and activity. (a) The higher the MTG-IFG connectivity (post emotion suppression RS minus post watch RS), the higher was subsequently reported exhaustion (emotion suppression minus watch condition). (b) There was a positive, yet nonsignificant correlation between IFG task activity (emotion suppression minus watch condition) and subsequently reported exhaustion (emotion suppression minus watch condition).

Relation of resting state connectivity and task activity to exhaustion

To control for baseline levels, the subjective exhaustion score for the watch condition was subtracted from the subjective exhaustion score for the emotion suppression condition. Likewise, post-watch connectivity values were subtracted from post-suppression connectivity values for areas which showed condition-induced connectivity differences (Fig. 3 & 4). Subjective exhaustion differences correlated highly positively and significantly with connectivity differences between the left MTG and the right IFG seed, r = .57, p = .002 (Fig. 5a). The correlation between subjective exhaustion differences and activity differences in the right IFG *during* the picture task (emotion suppression minus watch condition) was also positive and marginally significant, r = .35, p = .065 (Fig. 5b). Next, a multiple linear regression was calculated to compare the predictive value of IFG task activity and MTG-IFG connectivity for subjective exhaustion. A significant regression

equation was found ($F(2, 25) = 7.39$, $p = .003$) with an R^2 (explained variance) of .37. However, only MTG-IFG connectivity was a significant predictor of subjective exhaustion (standardized $b = .51$, $t(25) = 3.13$, $p = .004$), whereas IFG task activity was not (standardized $b = .24$, $t(25) = 1.45$, $p = .159$). This indicates that subsequently reported exhaustion mainly depended on TPN connectivity after task engagement.

Discussion

Several areas associated with emotion regulation were activated during emotion suppression, including the right IFG. Regarding the TPN in the subsequent RS, the right IFG showed increased connectivity with the left MTG and the OFC after emotion suppression, whereas the control condition (simply watching emotional pictures) showed decreased connectivity in these networks. The DMN was not significantly affected by prior emotion suppression, yet in the watch condition, the DMN's extension to left and right IOC and fusiform gyri was significantly decreased. Increased connectivity of the left MTG with the right IFG might be related to effortful self-control exertion, since it was valid predictor of subjective exhaustion.

The IFG bilaterally and the left MTG are among the areas most consistently associated with emotion regulation in a series of meta-analyses (Buhle et al., 2014; Diekhof et al., 2011; Frank et al., 2014; Kohn et al., 2014). Specifically, the posterior part of the left temporal cortex, which is where connectivity changes were detected in the present study, has been associated with encoding of semantic and perceptual representations (Buhle et al., 2014). The IFG is considered to be a core area necessary for successful emotion regulation and self-control (Aron, Durston, et al., 2007; Hare et al., 2009; Tabibnia et al., 2011). Its role in emotion suppression may be to inhibit processing of perceptual features inducing an emotional response or to signal the need to inhibit to other brain areas (Kohn et

al., 2014). Thus, connections between the IFG and MTG may be central to emotion suppression and the connectivity increase found after emotion suppression relative to pre-task baseline may reflect sustained connections between areas heavily implicated in task processing.

As reported previously, the IFG has been reported to show decreased activity and decreased connectivity after self-control exertion (Friese et al., 2013; Persson et al., 2013; Wagner et al., 2013). The present findings suggest that depletion effects may arise because connectivity of the IFG with other task-related areas is at least partly sustained after the end of a self-control task. Thus, the IFG may have a temporarily reduced capacity to influence activity in other areas, which might be critical for a subsequent self-control task. This might explain why depletion effects especially occur when participants have to switch from one self-control task to another, a phenomenon which has been in lack of an adequate explanation so far (Kurzban et al., 2013). In line with this idea, a recent study found that after self-control exertion, functional connectivity during task performance between the IFG and task-relevant task-specific areas was decreased (Wagner et al., 2013).

The notion that sustained connectivity of the IFG with task-related areas may be related to self-control exertion effects is further supported by the predictive value of the MTG-IFG connectivity for subjective exhaustion in the present study. Interestingly, MTG-IFG connectivity changes after the task, but not IFG activity during the task, was a valid predictor of subjective exhaustion. On the one hand, this finding might suggest that even though task engagement is effortful, depletion effects are more closely related to lingering after-effects than to self-control exertion itself. On the other hand, it also seems likely that participants had a better introspective awareness during a RS than during task engagement or that the effect is due to recency, as the RS was closer to the questionnaire than the task on a temporal scale.

In addition to the left MTG, also the OFC showed changes in connectivity with the IFG after task engagement. However, these changes did not correlate with subjective exhaustion and were mainly due to a decrease in connectivity after the watch condition, which renders these findings less likely to be related to effortful emotion suppression. Instead, they suggest that the control condition, i.e. watching emotional pictures, has affected subsequent resting state as well. The OFC has been associated with the representation of values, such as reward, mainly in the context of decision making and adaptive behavior (Schoenbaum, Takahashi, Liu, & Mcdannald, 2011). Under the assumption that OFC-IFG connectivity changes are sustained effects from prior task engagement, one could speculate that the OFC was involved in evaluating the emotional pictures, and the relative decoupling of the OFC from the IFG in the watch condition might have occurred because participants were instructed not to regulate their emotional responses.

Effects in the DMN occurred because of connectivity alteration of the PCC seed with the IOC bilaterally in the watch condition. The detected area of the IOC, which extended into the fusiform gyrus, is associated with face and emotion perception, and linking visual stimuli to memory (Rossion, Schiltz, & Crommelinck, 2003; Vuilleumier & Pourtois, 2007). In each negative picture set, 11 out of 24 pictures showed faces and 6 additional pictures showed humans. Hence these areas were likely involved in visual stimulus processing. RS coupling of the fusiform gyrus and parts of the occipital cortex to the hippocampus after encoding have been shown to predict memory (Tambini, Ketz, & Davachi, 2010). The area's decoupling from the DMN might reflect continued memory consolidation processes in the watch condition, whereas emotion suppression is known to reduce memory formation (Binder et al., 2012; Richards & Gross, 2006).

Our findings of increased or sustained connectivity in central task areas are in line with RS studies of learning and memory consolidation (Albert et al., 2009; Stevens et al.,

2010). One study of mental exhaustion has also reported subsequently increased TPN connectivity (Evers et al., 2012). Other RS studies on mental exhaustion either did not report TPN connectivity at all (Pyka et al., 2009) or a connectivity decrease (Esposito et al., 2014), yet employed a much shorter task duration (Pyka et al., 2009) or a very different study design (Esposito et al., 2014). Furthermore, these studies found no changes in the DMN after mental effort (Evers et al., 2012) or an enhancement (Esposito et al., 2014; Pyka et al., 2009). However, DMN enhancement effects were either too weak to survive correction for multiple comparisons (Esposito et al., 2014) or were detected in the absence of a pre-task RS (Pyka et al., 2009). When only analyzing the post-task RS, the present findings could be interpreted misleadingly as an enhancement and extension of the DMN to additional areas. The comparison to the baseline condition (pre-task RS) revealed that the increase in DMN connectivity in the emotion suppression condition was small and nonsignificant, yet there was a significant decrease in the watch condition. Thus RS connectivity is not only susceptible to prior effortful task engagement, but also to control tasks that feature emotional stimulus material, but no regulation instructions. These findings point to the importance of pre-manipulation RS assessments to be able to adequately interpret the data.

A limitation of the current study is that effects of emotion suppression during the task were rather weak and could only be detected based on the a priori definition of an area of interest, which did not survive correction for multiple comparisons. Yet, subsequent RS still showed clear effects of prior task engagement. Furthermore, the current study did not measure any effects of self-control exertion on behavior. This is a problem inherent to the study design, which allowed to examine sustained effects of prior effort

(self-control exertion) directly, i.e. in the absence of task engagement. Periods of rest hamper depletion effects (Baumeister, 2002), thus an additional task after the RS should have shown no or weakened depletion effects.

To our knowledge, this is the first study which examined effects of effortful emotion regulation on subsequent RS. It could be shown that engaging in emotion regulation as well as the unregulated experience of emotions have various effects on the TPN and the DMN in a subsequent RS. A new perspective on the potential mechanisms of depletion effects is provided. Areas critically involved in regulation and control, such as the IFG, exhibit sustained connectivity with previously regulated areas, here the left MTG, which might temporarily reduce the flexibility of the brain to adjust to new regulatory demands. Future studies on self-control exertion could extend on these findings by examining functional connectivity during ongoing task performance.

2.3 Third study: No effect of self-control exertion on amygdala reactivity and emotional memory

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Third study: No effect of self-control exertion on amygdala reactivity and emotional memory

Abstract

Self-control is critical for regulating impulsive behavior. Initial acts of self-control lead to impaired subsequent self-control performance. Wagner and Heatherton (2013) reported that acts of self-control impair prefrontal regulation of emotional reactivity, resulting in increased amygdala activation in response to emotional pictures. The amygdala is central to emotional memory formation. Here, we aimed at showing that increases in amygdala activation after self-control exertion lead to increased emotional memory. Fifty-two participants watched emotional and neutral pictures before and after they did or did not exert self-control during well-established self-control tasks, while brain activity was recorded with functional magnetic resonance imaging. Twenty-four hours later, participants recalled pictures in a surprise recall test. In contrast to the previously reported findings, exerting self-control did not increase amygdala activation in response to emotional pictures. Consequently, emotional memory was unaffected by self-control exertion. Independent from the self-control manipulation, viewing of emotional pictures resulted in higher amygdala activity, higher arousal ratings and better recall performance as compared to neutral pictures. While these results replicated findings from emotional memory research, exerting self-control had no influence on these variables. We conclude that increased amygdala reactivity in response to emotional cues may not be a reliable consequence of self-control exertion.

Keywords: Self-control, ego depletion, emotional memory, fMRI

Introduction

Self-control is the ability to control dominant responses such as impulses, thoughts, emotions, and action tendencies. It is key to achieving long-term goals such as academic achievement, stable social relationships, and mental and physical health

(Duckworth, 2011; Moffitt et al., 2011). Self-control failures, by contrast, contribute to many societal problems, including obesity, addiction, poor financial decisions, sexual infidelity, and gambling (Baumeister & Heatherton, 1996; Heatherton & Wagner, 2011).

The strength model of self-control postulates that any kind of self-control relies on a domain-independent, limited resource which becomes temporarily depleted with use (Baumeister, 2014; Muraven & Baumeister, 2000). Even though the mediating processes are not yet well understood (Beedie & Lane, 2012; Inzlicht et al., 2014; Inzlicht & Schmeichel, 2012; Job et al., 2010; Kurzban et al., 2013), ample evidence suggests that the initial exertion of self-control leads to impairments in subsequent tasks requiring self-control, decision making, and executive functioning (see Hagger, Wood, Stiff, & Chatzisarantis, 2010, for a meta-analysis).

Interestingly, emotion regulation apparently draws on the same underlying psychological processes as does the exertion of self-control. That is, the effortful inhibition of emotions leads to reduced persistence (Baumeister et al., 1998), poorer intellectual performance (Schmeichel, Vohs, & Baumeister, 2003), and an increased influence of impulsive processes on eating unhealthy food and drinking alcohol (Friese, Hofmann, & Wänke, 2008). In addition to impairing subsequent self-control exertion, emotion regulation is also affected by the previous exertion of self-control in seemingly unrelated tasks: After thought suppression (Muraven et al., 1998), a working memory task (Schmeichel, 2007), or managing one's impression in front of a skeptical audience (Vohs, Baumeister, & Ciarocco, 2005), the suppression of facial reactions during an emotive videotape was impaired.

On the neural level, Wagner and Heatherton (2013) recently reported that activation of the amygdala was increased after exertion of self-control during viewing of negative emotional pictures. The amygdala is one of the most important regions for emotional

processing in the brain (LeDoux, 2007). In addition, functional connectivity between the left amygdala and the ventromedial prefrontal cortex (VMPFC) was reduced as compared to the control group that did not engage in self-control. The VMPFC and lateral prefrontal brain areas are associated with the top-down regulation of emotional responses (Frank et al., 2014). Based on these results, the authors suggested that exerting self-control reduces the ability to spontaneously down-regulate emotional responses as indicated by an increased activation of the amygdala.

The amygdala is not only involved in emotional processing, but activity in this brain region is also critical for memory of emotional experiences, probably by modulating processes of plasticity in adjacent temporal lobe areas including the hippocampus (LaBar & Cabeza, 2006; McGaugh, 2004). Emotional experiences are typically better remembered than neutral ones (LaBar & Cabeza, 2006), and increased amygdala activity at the time of encoding predicts better recall (Kensinger & Corkin, 2004; McGaugh, 2004). The memory-facilitation effect of emotional material does not occur in persons with lesions to the amygdala (Cahill, Babinsky, Markowitsch, & McGaugh, 1995) and is reduced in persons who down-regulate their emotional responses during encoding (Binder et al., 2012).

As self-control exertion has been shown to impair emotion regulation and increase amygdala reactivity (Muraven et al., 1998; Schmeichel, 2007; Vohs et al., 2005; Wagner & Heatherton, 2013), here we aimed at showing that prior self-control exertion improves emotional memory via increased amygdala activation. Participants saw a series of emotional and neutral pictures before and after two tasks either requiring or not requiring self-control while their brain activity was recorded using functional magnetic resonance imaging (fMRI). The next day, participants engaged in a surprise recall task of the pictures they had seen. We expected stronger emotional reactivity in the amygdala after self-control exertion, especially for negative pictures (H1, see Wagner & Heatherton, 2013). Most

centrally, we expected better recall of emotional, especially negative pictures due to the increased emotional reactivity in the amygdala after self-control exertion (H2). Unexpectedly, no self-control exertion effects were found in the amygdala (H1), thus failing to conceptually replicate Wagner and Heatherton's (2013) findings. Consequently, there was also no evidence for better recall of emotional pictures (H2).

Methods

Participants

A total of 63 healthy participants completed the study. Eleven participants had to be excluded from the analysis due to excessive head movements during the scanning periods (threshold > 3 mm translation or > 2 degrees rotation, $n = 7$) and technical problems with fMRI data acquisition ($n = 4$). The final sample consisted of 52 participants (30 female) with a mean age of 24.50 years ($SD = 3.43$). Participants were randomly assigned to either the self-control exertion ($n = 26$) or the control condition ($n = 26$). The sample size was chosen to be similar to the study by Wagner and Heatherton (2012, $n = 24$ per group) and follows the guidelines of Simmons, Nelson, and Simonsohn (2011) who recommended a minimum of 20 participants per condition. Written informed consent was obtained from all participants who received CHF 25/hour (approximately U.S. $25). The local ethics committee approved the study.

Procedure

First, participants briefly practiced all tasks outside of the fMRI scanner. Next, they were positioned in the scanner and their head was secured in the coil. During scanning, they first engaged in a task where they watched pictures of positive, neutral, and negative

emotional valence. Next, they performed two self-control manipulation tasks that either required or did not require self-control (i.e. work on congruent vs. incongruent trials in a Stroop task, engage in free thought vs. thought suppression). Then they completed a second picture task with a different picture set. Figure 1 provides an overview of the fMRI session. Finally, participants filled out questionnaires including a manipulation check and demographic data. Participants returned 24 hours later for an unexpected free recall test of the pictures. After that, participants were debriefed and thanked.

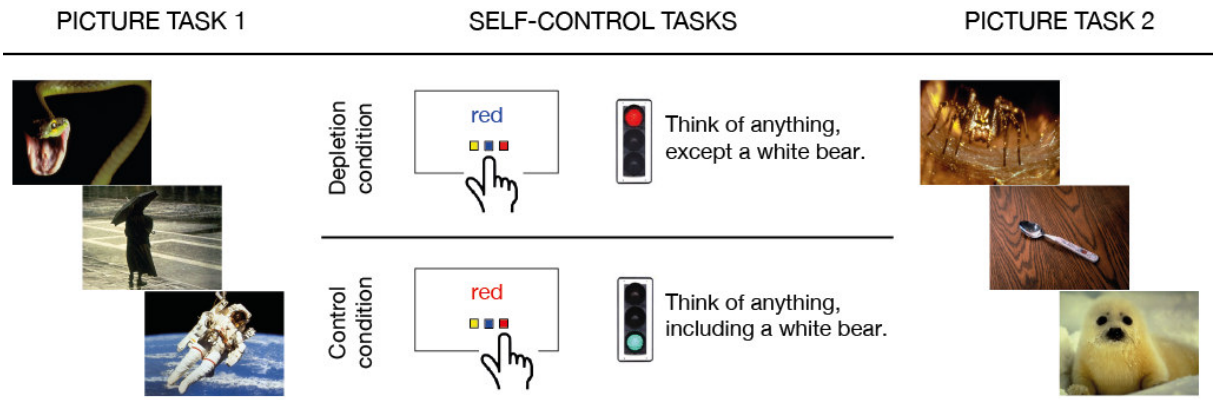

Fig. 1. Overview of the fMRI session. The first picture task served as a baseline measurement for emotional reactivity. Participants then either engaged in two depleting self-control tasks (Stroop, thought suppression) or two control tasks. Finally they completed another picture viewing task with a different set of pictures. The order of the two picture sets was counterbalanced between participants. 24 hours later, participants had to shortly describe each picture in a surprise free recall test.

Tasks

Picture task. Participants viewed a series of emotionally negative, neutral, and positive pictures (24 per valence category) and rated their arousal after each. Two sets of 72 pictures were chosen from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008). The order of the sets was counterbalanced across participants

and the order of the pictures within a set was pseudorandomized. Additionally, two neutral pictures were shown at the beginning and at the end of both picture tasks. These pictures were discarded from analyses to control for primacy and recency effects on memory. Each trial consisted of a jitter (0 – 2.5 s), a fixation cross (0.5 s), presentation of a picture (2 s), blank screen (1 s), presentation of a 4-point Likert scale to rate arousal (max. 2.5 s) and a display of their response (0.5 s). At the end of a trial, three dots appeared in the center of the screen for a variable amount of time (M = 4.72 s, SD = 1.09 s, range 1.37 to 8.02 s). This short break served to measure baseline activity. Task duration was approximately 12.5 min.

Stroop task. The task consisted of colored and white trial blocks. Before each block, three X's (XXX) in either colored or white letters cued what block type followed. In colored blocks, color words appeared in the center of the screen written in blue, red, or yellow letters. Participants were instructed to indicate the color of the letters by button press and ignore the semantic meaning of the word. In the self-control exertion condition, all trials were incongruent such that the semantic meaning of the word and color of the letters did not match. One quarter of the trials consisted of underlined words. In these cases, participants had to respond to the semantic meaning of the word instead of the color of the letters. Underlined words served to make the self-control exertion more demanding and to prevent participants from developing strategies to make the task easier (e.g., blurring vision). In the control condition, all colored trials were congruent (i.e., the color of the letters matched the semantic meaning of the word). In white blocks, trials consisted of the words blue, red, and yellow written in white letters. Participants had to indicate the semantic meaning of each word. White trials were used to measure baseline activity. In all trials, stimuli remained on screen until a button was pressed or until 1500 ms had passed. The duration of a following fixation cross was adjusted such that each trial was

2200 ms long (response time after stimulus presentation plus fixation cross). Each block consisted of 12 trials. There were 20 blocks in total, 15 of which employed colored trials, and 5 employed white trials. Task duration was approximately 9 min.

Thought-suppression task. The second task to manipulate self-control exertion was a thought-suppression task (Mitchell et al., 2007; Wegner, 1989). In the self-control exertion condition, participants were shown a red light at the beginning of each block, which signaled that they had to suppress any thoughts about a white bear during the following block. The traffic light was presented for 2 s and was followed by a black screen of 30 s duration. In the control condition, participants were shown a green traffic light and instructed to think freely of anything, including a white bear. At the end of each block, a fixation cross appeared for a variable amount of time (11 - 20 s), during which all participants were instructed to think freely of anything they wanted. The task consisted of 10 blocks and lasted for approximately 8 min.

Free recall task. Participants had to describe from memory as many of the pictures as possible that they had seen during the fMRI session the previous day. They were asked to indicate for each picture whether it had been presented in the first or second picture task. None of the participants indicated that she or he suspected a recall task for the second day.

Manipulation check

Participants answered three questions relating to the Stroop and the thought suppression/free thought task, asking how exhausting and how difficult they found the task, and how much concentration it demanded. An effort mean score was calculated over all six items (Cronbach's $\alpha = 0.73$).

Functional imaging

MRI scanning was performed on a Philips Intera 3 T wholebody MR unit equipped with an eight-channel Philips SENSE head coil at the University Hospital of Zurich, Switzerland. Functional time series were acquired with a sensitivity encoded, single-shot echo-planar sequence (SENSE-sshEPI) sensitive to BOLD contrast (T2* fast field echo with the following acquisition parameters: TR (repetition time) = 2500 ms, TE (echo time) = 35 ms, FOV (field of view) = 220 mm, acquisition matrix = 80 x 80, interpolated to 128 x 128, voxel size: 3.3 x 3.3 x 3.3 mm^3, no gap and SENSE acceleration factor R = 2). By using a midsagittal scout image, 40 contiguous axial slices were placed to the anterior–posterior commissure plane covering the entire brain. The picture tasks consisted of approximately 300 functional scans each. Participants viewed stimuli through a mirror mounted on top of the head coil.

Data analysis

Repeated-measures ANOVAs with the within-subjects factors picture valence (negative, neutral, positive) and time (1^{st} set, 2^{nd} set) and the between-subjects factor self-control condition (self-control exertion, control) were used to test for effects of the experimental manipulation. This analysis was applied to arousal ratings, recall performance, and brain data.

MATLAB Release 2012b and SPM8 (www.fil.ion.ucl.ac.uk) were used for fMRI data analysis. Functional images were corrected for differences in acquisition time between slices and realigned to correct for head movement. Participants' individual T1-weighted structural image was co-registered with the mean functional image and normalized to the standard T1 MNI template using the new-segmentation-procedure. Functional images were normalized to the standard MNI template using the same transformation and spatially resampled to 2x2x2mm voxels. Finally, images were spatially smoothed using an

8mm FWHM Gaussian kernel. A 128-s-cutoff high-pass filter was added to the confound partition of the design matrix to account for low-frequency drifts, and a correction for intrinsic autocorrelations was included in the analysis.

For the analysis of the self-control manipulation tasks, two additional participants had to be excluded because of too much movement during these tasks only. A General Linear Model (GLM) was set up for both tasks combined. Stroop parameters included correct color trials (self-control exertion condition: incongruent and underlined trials, control condition: congruent trials), correct white trials, incorrect trials, and button presses. Parameters from the thought-suppression task included task blocks (thought suppression vs. free thought) and fixation blocks. In addition, six movement parameters derived from realignment correction served as regressors of no interest. The contrasts color trials versus white trials (Stroop task) and task blocks versus fixation blocks (thought-suppression task) were used for group analyses. Differences between the self-control exertion and the control condition were examined using *t*-tests, with a specific focus on the inferior frontal gyrus, which is critically involved in self-control and inhibition (Aron et al., 2004; Tabibnia et al., 2011). A sphere of 6 mm around peak coordinates of differences for each task was used to extract activity from the inferior frontal gyrus and compare it with the effort mean score.

For each of the two picture tasks, a GLM was set up with regressors of the onsets of negative, neutral, and positive pictures, baseline periods, button presses, and movement parameters. Three contrast images were calculated comparing negative, neutral, and positive picture presentations to baseline periods and analyzed differences between conditions on the group level using ANOVAs. A fourth contrast compared emotional (neg-

ative and positive) pictures to neutral ones. Based on a priori hypotheses, we were particularly interested in the amygdala because of its central function in emotional processing (Phelps, 2006).

In addition, differences in functional connectivity between conditions were investigated using a generalized form of psychophysiological interaction (gPPI) analysis (McLaren, Ries, Xu, & Johnson, 2012). In contrast to standard PPI, gPPI allows to incorporate psychophysiological interaction regressors for all conditions into one model. Analogously to Wagner and Heatherton (2013), a six millimeter sphere in the left amygdala (center coordinates in MNI space: -21, -6, -21) was used as seed to extract the first eigenvariate time-series. A second time-series was extracted from the right amygdala (6 mm sphere centered on 22 -2 18). Psychophysiological interaction regressors for negative, neutral, and positive pictures and baseline periods were then included in two GLMs for the left and right amygdala together with the respective psychological regressors, the original time-series and nuisance regressors. Contrasts for negative, neutral, and positive pictures versus baseline periods were submitted to group analyses.

Another GLM was set up to test effects of successful memory encoding. Regressors were correctly recalled pictures (M = 23.52, SD = 9.93, range = 5 - 49), forgotten pictures, button presses, baseline periods, and movement parameters. Contrast images of recalled versus forgotten pictures were subjected to the group analysis. To test specifically for effects of emotional memory, an additional regression analysis was conducted. The difference between the amount of recalled emotional versus neutral pictures was used as a regressor to predict brain activity in the contrast images emotional versus neutral pictures from the first GLM. In all memory-related analyses, the hippocampus was an a priori area of interest in addition to the amygdala. WFU pickatlas was used to define these areas

anatomically (Maldjian et al., 2004; Tzourio-Mazoyer et al., 2002). Small-volume-corrections (SVC) was applied at a threshold of $p < 0.05$ (corrected for the volume of interest), building on an initial threshold of $p < .001$ (uncorrected) for the whole brain. Anatomical labels were assigned with the AAL toolbox (Tzourio-Mazoyer et al., 2002).

Results

Manipulation Check

As expected, participants in the self-control exertion condition ($M = 4.14$, $SD = 1.06$) found the self-control tasks more exhausting, more difficult, and demanding more concentration than participants in the control condition ($M = 3.26$, $SD = 1.07$), $t(50) = 2.97$, $p = .005$.

In addition to these self-reports, brain activity during the tasks was checked for differences due the self-control manipulation (i.e. Stroop task, thought-suppression task). In both tasks, brain areas related to effortful self-control were more activated in the self-control exertion condition than in the control condition: Comparison of the self-control exertion condition and the control condition in the Stroop task revealed stronger activity in prefrontal areas, the basal ganglia, and other areas commonly activated in this task (see Supplementary Table S1 for detailed information). The thought-suppression condition led to stronger activity than the control condition in prefrontal areas, the cingulate cortex, and the basal ganglia (see Supplementary Table S2). The left inferior frontal gyrus, a region commonly implicated in the exertion of top-down control, was more activated in the self-control exertion condition than in the control condition in both tasks. In addition, the averaged activity in the inferior frontal gyrus of both tasks correlated significantly with

the behavioral effort mean score (r = .34, p = .015). Together with the results on self-reported effort, these data suggest that our self-control exertion manipulation was successful.

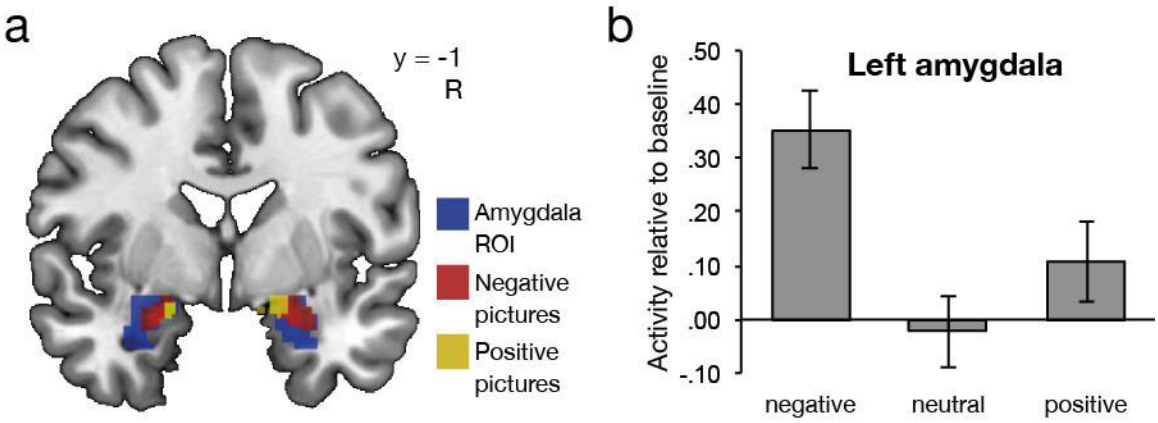

Fig. 2. No self-control exertion effect on emotional arousal ratings, amygdala activity and memory for pictures. The graphs show the change scores of the second picture viewing task minus the first picture viewing task (baseline) for arousal ratings (a), amygdala activity (b), and free recall (c). Error bars indicate standard errors of the mean.

Arousal ratings

As expected, arousal ratings of the pictures differed between the three emotional categories (negative, neutral, positive,). A repeated-measures ANOVA with the within-subjects factors emotional valence and time and the between-subjects factor self-control condition only showed a significant main effect of picture valence (F(2, 100) = 336.66, p < .001). Negative pictures received the highest arousal ratings (M = 2.98, SD = 0.58), as compared to positive (M = 2.16, SD = 0.60, p < .001) and neutral pictures (M = 1.46, SD = 0.46, p < .001), while neutral pictures received the lowest (compared to positive and neutral pictures, both ps < .001; see Fig. 2a). There was a tendency to lower arousal ratings for the later picture set (F(1, 50) = 3.29, p = .076) possibly reflecting adaption processes.

The main effect of self-control condition ($F(1, 50) = 0.04$, $p = .845$) and the interactions of self-control condition and time ($F(1, 50) = 1.03$, $p = .315$) or self-control condition, time, and valence were non-significant ($F(2, 100) = 0.20$, $p = .820$).

Picture task

Emotional valence. An overall repeated-measures ANOVA of both picture tasks revealed a main effect of emotional valence in a widespread network including brain areas involved in processing of emotions (e.g. the amygdala) and emotion regulation (e.g., inferior frontal gyrus; Table 1). Anatomically defined ROIs were used to extract activity from the amygdala (Fig. 3a). As expected, the activity pattern mirrored that of the arousal ratings (Fig. 3b). Activity in the left amygdala was highest for negative pictures ($M = 0.35$, $SD = 0.55$), lowest for neutral ($M = -0.02$, $SD = 0.48$), and intermediate for positive pictures ($M = 0.11$, $SD = 0.53$). Differences between valences were highly significant (all ps < .001), replicating well-known findings (Phan, Wager, Taylor, & Liberzon, 2002; Rasch et al., 2009). In line with Wagner and Heatherton (2013), we focus on the left hemisphere for result reporting, but found a very similar pattern of results in the right hemisphere.

Table 1

Brain areas showing a main effect of emotional valence.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Middle temporal gyrus	6012	37	R	52	-68	4	Inf
Fusiform gyrus	9640	37	L	-40	-50	-18	Inf
Thalamus[1]	2891		L	-2	-30	-2	Inf
Insula[2]	1321		L	-40	18	-8	Inf
Inferior frontal gyrus PTR	1907	45	R	52	26	-2	Inf
Rolandic operculum	300	48	R	38	-18	18	7.50
Postcentral gyrus	1494	3	L	-42	-30	60	7.20
Middle frontal gyrus[3]	297	46	L	-40	50	-2	7.02
Superior temporal gyrus	256	22	R	60	-12	4	6.51
Precentral gyrus	263	4	R	38	-20	50	6.29
Superior temporal gyrus	179	41	L	-46	-32	12	6.19
Angular gyrus	52	39	R	46	-62	38	5.89
Anterior cingulate cortex	87	10	L	-4	54	-2	5.83
Inferior frontal gyrus TPR	21	45	L	-46	28	30	5.71
Inferior parietal gyrus	26	3	L	-52	-24	40	5.27

Note. List of brain areas showing a main effect of emotional valence based on an F-contrast, thresholded at $p < .05$ (FWE corrected for the whole brain) in a minimum of 20 adjacent voxels. [1]This cluster incorporates amygdala and hippocampus, both bilaterally. [2]52% of this cluster lie in the left inferior frontal gyrus. [3]47% of this cluster lie in the left inferior frontal gyrus. BA, Brodmann area; R, right hemisphere; L, left hemisphere, PTR, triangular part.

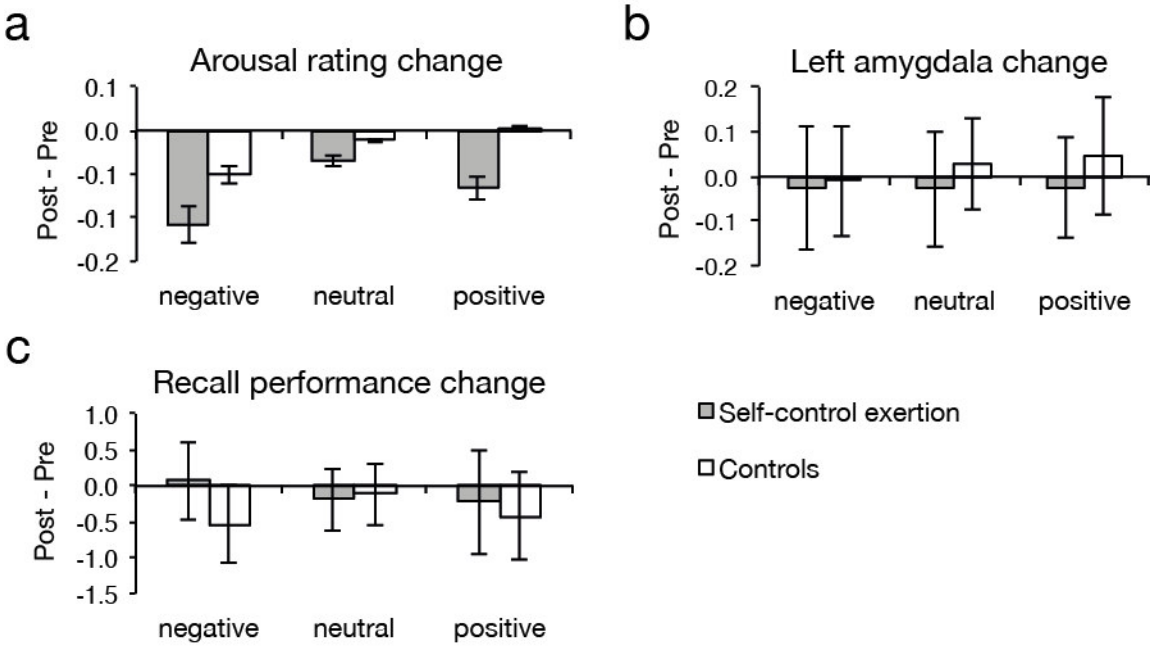

Fig. 3. Effects of emotional valence on amygdala activity. (a) Frontal brain view depicting the bilateral amygdala ROI, negative and positive pictures relative to baseline activation (in this order of superposition), thresholded at $p < .001$ (uncorrected). Activation is superimposed on a canonical normalized image. (b) Mean activation extracted from the left amygdala ROI elicited by negative, neutral and positive pictures, relative to baseline activation. Error bars indicate standard errors of the mean.

Effects of self-control exertion. To test for effects of self-control exertion, interactions between self-control condition, time, and emotional valence were examined in a repeated-measures ANOVA. No significant interaction was observed when family-wise error correction was applied for the whole brain. The analysis was repeated for the amygdala ROI. Different from Wagner and Heatherton (2013) and against our expectations (H1), no significant differences were detected in the amygdala ($F(2, 100) = 0.08$, $p = .928$, Fig. 2b). Thus, in the present study, self-control exertion had no effect on emotional reactivity, as indicated by amygdala activity. In an exploratory analysis of the whole brain, the VMPFC (Fig. 4a) and the anterior cingulate cortex showed interaction effects at a lower threshold of $p < .001$ (uncorrected; see Table 2 for details). When comparing negative

versus neutral pictures, the effect was strongest for the VMPFC, which is implicated in emotion regulation (Johnstone, van Reekum, Urry, Kalin, & Davidson, 2007; Ochsner et al., 2012; Urry et al., 2006). Activity in the VMPFC decreased after the self-control exertion tasks, while it increased slightly after the control tasks (Fig. 4b). Interestingly, Wagner & Heatherton (2013) did not report reduced activity of the VMPFC, but a reduced connectivity between this area and the amygdala after self-control exertion for negative pictures. For positive vs. neutral pictures in the present study, the effect was reversed in the medial frontal gyrus and anterior cingulate cortex (see Table 2).

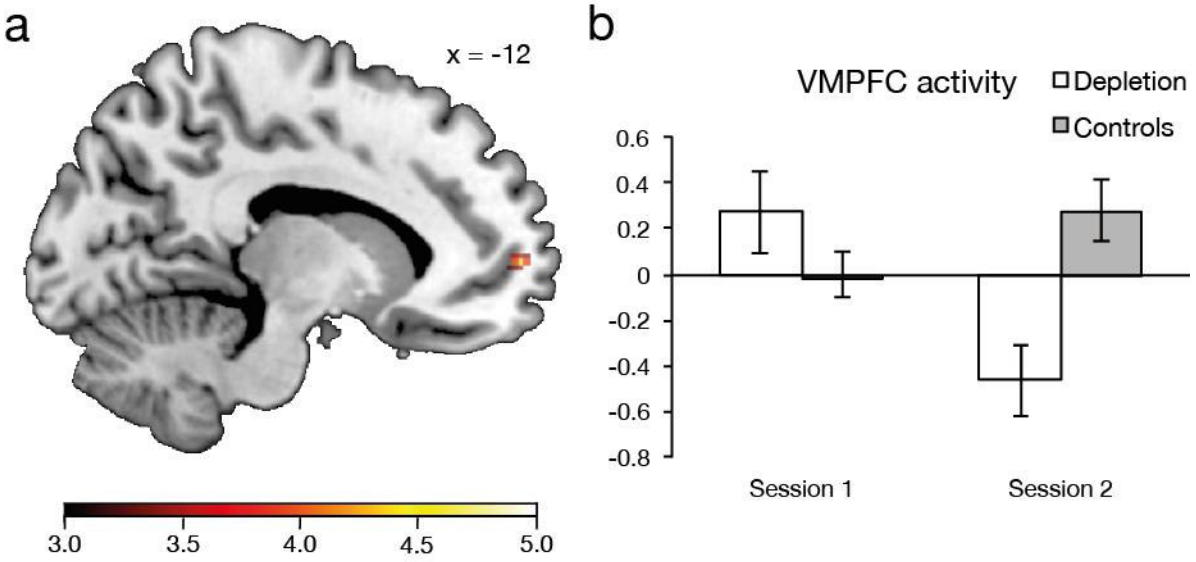

Fig. 4. Self-control exertion effects in the ventromedial prefrontal cortex (VMPFC). (a) Sagittal view of the VMPFC cluster with color-coded *T*-values, thresholded at $p < .001$ (uncorrected), superimposed on a canonical normalized image. (b) The extracted cluster from the VMPFC (cluster size k =20) shows the expected effect of self-control exertion: After the self-control exertion tasks, activity decreased. After the control tasks, activity increased slightly, potentially reflecting adaptation processes to task demands.

Table 2

Brain areas showing an interaction effect of time, self-control condition, and emotional valence.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Negative versus neutral: Reduced activation after self-control exertion							
Medial frontal gyrus[1]	20		L	-12	60	4	4.36
Putamen	43		R	30	-16	2	4.17
Lobule IV, V of vermis	20		L	-6	-54	-26	4.04
Negative versus neutral: Interaction of time and condition testing for activation							
No suprathreshold clusters							
Positive versus neutral: Interaction of time and condition testing for deactivation							
No suprathreshold clusters							
Positive versus neutral: Increased activation after self-control exertion							
Anterior cingulate cortex	44		L	-10	4	30	4.35
Anterior cingulate cortex	32		L	-12	26	18	4.16
Medial frontal gyrus	54			0	48	34	4.01
Medial frontal gyrus	29		L	-6	30	52	3.56

Note. List of brain areas showing interaction effects, thresholded at $p < .001$ (uncorrected) in a minimum of 20 adjacent voxels. No activation survived whole-brain correction. [1]The medial frontal gyrus forms part of the VMPFC. BA, Brodmann area; R, right hemisphere; L, left hemisphere.

For the connectivity analysis using the gPPI approach with the amygdala seeds, interactions between self-control condition, time, and emotional valence were again computed. In contrast to Wagner and Heatherton (2013), no connectivity changes for either the left or right amygdala were found that lay within the VMPFC or that survived correction for multiple comparisons.

Memory

Recall performance. Emotional valence had a significant impact on memory performance in the surprise free recall test on the next day ($F(2,100) = 38.60$, $p < .001$). Negative ($M = 4.10$, $SD = 1.14$) and positive pictures ($M = 5.05$, $SD = 1.27$) were better remembered than neutral ones ($M = 2.62$, $SD = 1.02$, both ps $< .001$), replicating the well-known modulating effect of emotion on memory (see McGaugh, 2000). In contrast to our hypothesis (H2), but logically following the null-effect of self-control exertion on amygdala reactivity, self-control exertion had also no effect on recall performance (Fig. 2c). Neither the three-way interaction between time, emotional valence, and self-control condition ($F(2, 100) = 0.21$, $p = .812$) nor the two-way interaction between time and self-control condition was significant ($F(2, 100) = 0.26$, $p = .615$). Thus, the current study is unable to provide evidence for a self-control exertion effect on memory formation.

Effects of neural activity on memory. Since self-control exertion did not affect memory, it comes as no surprise that brain activity related to successful memory encoding did not show any changes after self-control exertion. Next the two experimental groups and the two picture sets were combined to investigate brain activity predicting recall. Recalled pictures as compared to forgotten ones elicited stronger activity bilaterally in the hippocampus (left: [-18 -4 -20], $Z = 4.80$, p(SVC) = .001; right: [16 -4 -16], $Z = 4.80$, p(SVC) = .001, see Figure 5a) and the amygdala (left: [-18 -4 -18], $Z = 4.77$, p(SVC) <

.001; right: [18 -2 -16], Z = 4.64, p(SVC) < .001). Further areas are reported in Supplementary Table S3. A regression analysis revealed that the left hippocampus contributed to the emotional memory effect ([-30 -22 -16], Z = 3.90, p(SVC) = .017, see Figure 5b and c). These results confirm relationships well-known from extant literature: Successful memory encoding critically depended on the hippocampus and the amygdala (McGaugh, 2004; Squire, 1992).

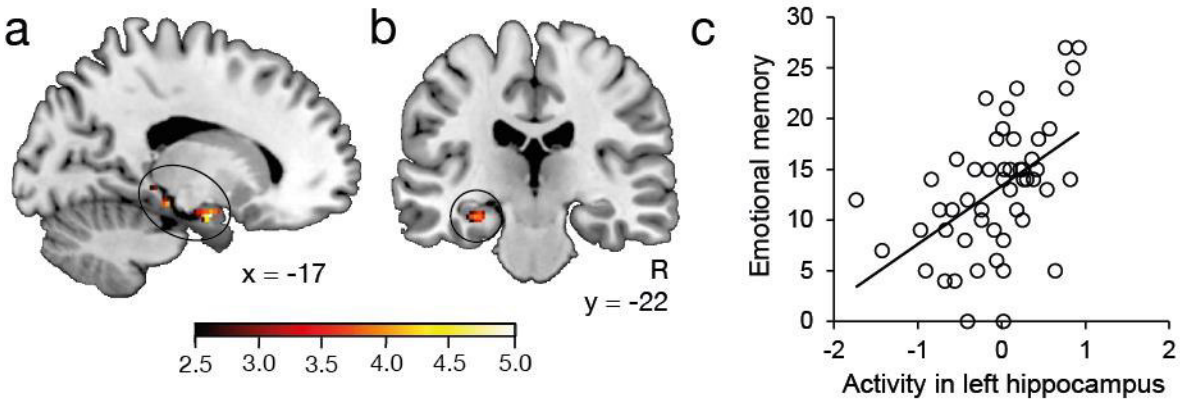

Fig. 5. Effects of memory on neural activity. (a) Areas in the hippocampus and the amygdala which were more strongly activated during correctly recalled as compared to forgotten pictures (subsequent memory effect). (b) Regression analysis revealed that higher activity in the left amygdala predicted higher emotional memory performance (i.e., number of correctly remembered emotional minus neutral pictures) tested 24 h later. For illustration purposes, T-values are color-coded at a threshold of p < .005 (uncorrected) and activations are superimposed on a canonical normalized T1 image. (c) The scatter plot shows the activity in the left hippocampus cluster which predicts emotional memory performance tested 24 hours later.

Discussion

The current study examined self-control exertion effects on emotional memory. We assumed that emotional pictures would be remembered better after self-control exertion as a consequence of the heightened amygdala activity during encoding. Behavioral,

neural, and memory-related data revealed expected and typical effects of emotional valence. The self-control exertion tasks were rated as more effortful than the control tasks and heightened activity was found in prefrontal control areas during the self-control exertion tasks as compared to the control tasks, as expected. These findings suggest that our experimental manipulations and procedures were successfully implemented. However, in contrast to previous reports, self-control exertion did not affect amygdala reactivity and memory performance.

Replication is key for testing the reliability of effects and establishing trustworthy empirical results (Funder et al., 2014; J. P. a. Ioannidis, 2012; Simons, 2014). The replicability of self-control exertion effects has recently been questioned, and it has been argued that the medium-to-large effect sizes related to self-control exertion (Hagger et al., 2010) may partly arise from publication bias (Carter & McCullough, 2014). This notion underlines the need to conduct replication studies on self-control exertion effects. The current study included a conceptual replication of a self-control exertion effect on emotional processing. It is most directly related to an fMRI study from Wagner and Heatherton (2013). This study had shown increased activity in the left amygdala after self-control exertion. However, rather than an exact replication, the current study was designed to conceptually replicate and extend these findings. It thus differs from Wagner and Heatherton's work (2013) in several ways:

First, to manipulate self-control exertion Wagner and Heatherton (2013) used an attention control task where participants had to inhibit reading words which appeared on screen during a film while we used a thought suppression task and a Stroop task. Both the thought-suppression task (Fischer, Greitemeyer, & Frey, 2008; Friese, Schweizer, Arnoux, Sutter, & Wänke, 2014; Muraven et al., 1998) and the Stroop task (Bray, Martin Ginis, Hicks, & Woodgate, 2008; Job et al., in press; Vohs et al., 2005) used here have been

shown to induce self-control exertion effects previously (see also Hagger et al., 2010). Second, two self-control tasks were used instead of one, because research suggests that a series of different tasks leads to particularly strong self-control exertion effects (Vohs et al., 2013). Third, participants rated their arousal after each picture in our study, whereas in Wagner and Heatherton's study (2013), participants made unrelated "indoor or outdoor" judgements. It is conceivable that reflecting on emotional arousal while being exposed to the pictures made all participants focus on emotional processing to the same degree, potentially interfering with differences caused by previous self-control exertion. However, we have used the same task in previous research without any indication that it may have interfered with the advantage of emotional over neutral pictures in memory formation (Rasch et al., 2009). Other researchers have also employed arousal ratings of IAPS pictures and reported corresponding changes in amygdala activity (e.g. Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). In sum, while there are some differences in the study designs, we consider these unlikely to have precluded potential self-control exertion effects on emotional processing.

One aspect of the study where we followed Wagner and Heatherton (2013) is that participants were not instructed to regulate their emotional responses. It was assumed that they would engage in spontaneous emotion regulation upon seeing pictures of emotional valence. A limitation of this approach is that it is unclear to what degree participants actually did so and which emotion regulation strategies they used. Many brain imaging studies about emotion regulation have focused on "reappraisal" and reported activity increases in lateral prefrontal areas (Ochsner et al., 2012). However, regulating one's emotions by reappraisal apparently does not depend on effortful self-control, whereas voluntary emotion suppression does (Wang et al., 2014). The latter emotion regulation

strategy is associated with a reciprocal relationship between the VMPFC and the amygdala in the brain (Johnstone et al., 2007), and Wagner and Heatherton (2013) reported reduced connectivity between these brain areas after self-control exertion during assumed spontaneous emotion regulation during picture-viewing. While these connectivity changes were not replicated in the present study, self-control exertion decreased activity in the VMPFC during viewing of negative pictures. This finding might suggest that participants in the present study employed a less effortful emotion regulation strategy relying less strongly on the VMPCF and were thus less affected by self-control exertion. Note that decreases in VMPFC activity after self-control exertion were detected only after application of a rather liberal statistical threshold, therefore this finding should be interpreted with caution. Nevertheless, future studies on self-control exertion and emotion regulation could profit from an explicit instruction to suppress emotions, which has also been shown to undermine memory formation (Binder et al., 2012).

Finally, it should be noted that the analysis Wagner and Heatherton (2013) used to test for increased amygdala activity after self-control exertion was very liberal. It did not include a correction for multiple comparisons when testing for self-control exertion effects on brain activity. In addition, the reported specificity of the self-control exertion effect for negative pictures seems at least debatable as it appears there is a main effect of previous self-control exertion on all picture categories. Descriptively, increased amygdala activity was apparent for all, positive, neutral, and negative pictures in their study. The difference between conditions just only reached statistical significance for negative pictures. Further research on the reliability of effects of self-control exertion on emotional reactivity is definitely warranted.

The main extension of the present work beyond previous work was the investigation of self-control exertion effects on emotional memory. Since there was no self-control

exertion effect during encoding, it was only consequential that also no effect on emotional memory was found. In contrast, well-known memory effects were replicated, such that emotional information was better remembered than neutral ones, and that memory formation critically depended on activity in the hippocampus. The initial hypothesis remains open for a test. Provided increased reactivity in the amygdala after self-control exertion during encoding of emotional scenes, research on emotional memory formation would still predict a recall advantage for persons after having exerted self-control.

Conclusion

In sum, manipulation checks, arousal data, and neural activity during the self-control manipulation tasks indicate that the self-control exertion manipulation was successful. Nevertheless, there was no effect of self-control exertion on emotional processing and emotional memory thereafter. We conclude that increased amygdala activity in response to emotionally valenced stimuli is not a necessary consequence of prior self-control exertion.

Supplementary Material

Supplementary Table S1

Areas with higher activation during the Stroop task (self-control exertion condition) than during the control task.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Precentral gyrus	23577	32	L	-44	8	32	7.04
Inferior occipital gyrus		37	L	-42	-62	-12	6.99
Superior parietal lobule		7	L	-20	-58	42	6.97
Middle frontal gyrus	221	45	R	46	40	20	5.30
Inferior frontal gyrus PTR		45	R	42	30	28	4.38
Inferior frontal gyrus PTR		45	R	50	28	26	3.56
Inferior frontal gyrus POR	322	44	R	42	8	30	4.50
Middle frontal gyrus		6	R	50	10	44	3.57
Olfactory cortex	43	25		0	0	-10	4.28
Inferior frontal gyrus POR	24	11	L	-18	34	-4	4.24
Insula	168	47	R	32	28	0	4.21
Insula		48	R	28	30	12	4.07
Caudate nucleus	64	25		0	22	6	4.19
Caudate nucleus			L	-14	30	6	3.50
Middle frontal gyrus	62	46	L	-30	48	18	4.09
Anterior cingulate cortex	11	47	R	18	32	4	4.09
Middle frontal gyrus	9	6	L	-30	-20	62	3.67
Thalamus	18		L	-4	-24	14	3.49
Putamen	21	48	L	-28	8	-4	3.49
Putamen		48	L	-26	10	4	3.24

Third study: No effect of self-control exertion on amygdala reactivity and emotional memory

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	No. of *Z*
Middle frontal gyrus	8	46	R	38	44	28	3.36
Putamen	5		R	26	4	4	3.33
Thalamus	6		L	-2	-12	20	3.31
Left calcarine sulcus	8	17	L	-12	-76	12	3.26
Caudate nucleus	8		L	-6	4	18	3.24

Note. List of brain areas showing higher activity in the self-control exertion condition (incongruent trials vs. white baseline trials) than in the control condition (congruent trials vs. white baseline trials), thresholded at $p < .001$ (uncorrected) in a minimum of 5 adjacent voxels. Intendations indicate subpeaks within a larger area. BA, Brodmann Area, L, left, R, right, POR, pars orbitalis, PTR, Pars triangularis.

Supplementary Table S2

Areas with higher activation during thought suppression (self-control exertion condition) than during a control task.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Putamen	11		R	22	-6	12	3.95
Inferior frontal gyrus POR	7	47	L	-30	32	-10	3.76

Note. List of brain areas showing higher activity in the self-control exertion condition (thought suppression blocks vs. fixation) than in the control condition (free thought blocks vs. fixation), thresholded at $p < .001$ (uncorrected) in a minimum of 5 adjacent voxels. Intendations indicate subpeaks within a larger area. BA, Brodmann Area, L, left, R, right, POR, pars orbitalis.

Supplementary Table S3

Remembered vs. forgotten pictures.

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Inferior frontal gyrus POR	768	38	L	-40	26	-14	6.07
Inferior frontal gyrus PT		47	L	-46	18	0	5.18
Inferior frontal gyrus PT		47	L	-36	28	6	4.05
Medial frontal gyrus	2967	9	L	2	56	32	5.77
Medial frontal gyrus		32	L	-6	52	20	5.73
Medial frontal gyrus		9	L	-4	52	38	5.73
Pallidum	316		L	-10	-2	-8	5.19
Hippocampus		28	L	-18	-4	-20	4.80
Parahippocampus		27	L	-22	-30	-10	4.35
Middle frontal gyrus	293	44	L	-36	14	40	5.07
Middle frontal gyrus		8	L	-30	16	50	4.35
Middle frontal gyrus		6	L	-30	4	40	3.74
Precuneus	627		L	0	-64	34	5.07
Precuneus			L	-4	-56	32	4.79
Posterior cingulate cortex		30	R	4	-50	24	4.18
Hippocampus	147	34	R	16	-2	-16	5.06
Hippocampus		35	R	12	-16	-12	3.75
Parahippocampus		35	R	6	-18	-18	3.72
Inferior frontal gyrus POR	113	38	R	38	22	-18	4.92
Inferior frontal gyrus POR		38	R	42	32	-12	4.67
Inferior frontal gyrus POR		38	R	48	26	-10	3.50

Third study: No effect of self-control exertion on amygdala reactivity and emotional memory

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Angular gyrus	619	39	L	-46	-66	38	4.76
Angular gyrus		39	L	-46	-64	26	4.27
Angular gyrus		7	L	-40	-62	50	4.21
Thalamus	368		L	-4	-12	6	4.72
Thalamus			L	-2	-24	8	4.58
Caudate nucleus		25	L	8	8	0	4.26
Inferior frontal gyrus PTR	191	47	R	48	24	-2	4.45
Inferior frontal gyrus PTR		48	R	40	26	10	3.47
Fusiform gyrus	467	37	R	40	-56	-20	4.38
Inferior occipital cortex		19	R	36	-72	-10	4.29
Fusiform gyrus		37	R	40	-60	-12	4.06
Cerebellum crus I	78		L	-26	-74	-28	4.79
Caudate nucleus	37		L	-12	2	10	4.28
Pallidum			L	-20	0	6	3.28
Middle temporal gyrus	75	37	L	-50	-58	0	4.19
Supramarginal gyrus	60	40	L	-58	-48	32	4.17
Supramarginal gyrus		22	L	-58	-50	24	3.47
Middle frontal gyrus	113	44	R	40	10	42	4.06
Middle frontal gyrus		9	R	48	16	42	4.06
Caudate nucleus	25		R	14	18	4	4.43
Calcarine sulcus	30	17	R	14	-84	4	4.42
Fusiform gyrus	68	37	L	-36	-54	-16	3.95
Angular gyrus	97	39	R	38	-56	28	3.87
Angular gyrus		39	R	42	-60	38	3.75
Angular gyrus		39	R	32	-50	24	3.44

Third study: No effect of self-control exertion on amygdala reactivity and emotional memory

Region	No. of voxels	BA	L/R	MNI coordinates *x*	*y*	*z*	*Z*
Inferior occipital cortex	110	19	L	-36	-78	-12	3.85
Middle occipital cortex		19	L	-40	-76	0	3.27
Pallidum	18		R	20	-2	8	3.84
Anterior cingulate cortex	29	24	L	2	30	20	3.81
Anterior cingulate cortex	5		R	6	8	26	3.75
Fusiform gyrus	6	37	R	36	-46	-22	3.75
Middle cingulate cortex	23	23	R	2	-14	40	3.74
Olfactory cortex	21	48	R	30	10	-12	3.72
Putamen		48	R	34	0	-10	3.24
Fusiform gyrus	28	18	R	24	-80	-12	3.70
Anterior cingulate cortex	12		R	6	16	22	3.65
Inferior frontal gyrus POR	19	47	L	-46	38	-4	3.61
Supramarginal gyrus	15	48	R	54	-48	28	3.60
Middle temporal gyrus	10	37	L	-44	-70	14	3.44
Middle occipital gyrus	9	19	L	-46	-76	-2	3.37
Angular gyrus	6	7	R	36	-62	52	3.36
Putamen	8	48	L	-30	4	-6	3.35
Middle cingulate cortex	11	23	L	-2	-28	36	3.29

Note. List of brain areas which were more activated during pictures which were later remembered than forgotten in the free recall task, thresholded at $p < .001$ (uncorrected) in a minimum of 5 adjacent voxels. Intendations indicate subpeaks within a larger area. BA, Brodmann Area, L, left, R, right, POR, pars orbitalis, PTR, Pars triangularis.

3 Discussion

3.1 Revisiting the studies

First study: When white bears and money influence self-control

For the publication manuscript, we have focused on comparing our results to one specific motivational model, the process model. First, I will discuss our findings in light of three other self-control models, the opportunity cost model (Kurzban et al., 2013), the labor/leisure tradeoff model (Kool & Botvinick, 2014), and the resource allocation model (Beedie & Lane, 2012). Then I will compare this study to other brain imaging studies.

According to the opportunity cost model, the thought-suppression task of our experiment has bound more computational mechanisms than the control task. This resulted in opportunity costs, i.e. the computational mechanisms could not be deployed for other mental processes. The opportunity costs induced the subjective experience of effort, and thus lowered the motivation to deploy computational mechanisms for the subsequent Stroop task. Providing monetary incentives means that there are additional benefits related with task engagement. Conclusively, self-control exertion increases the costs of further self-control acts, while incentives increase the benefits. In the framework of this model, brain activity changes, such as the ones found in the left IFG, should relate to changes in the deployment of computational mechanisms. This function could be attributed to the IFG. The increased activity in the high-motivation depletion condition would mean that the incentive-induced benefits outweighed the costs originating from prior task engagement. Then IFG activity should have increased even further or at least as much in highly motivated non-depleted participants as in highly-motivated depleted participants. However, activity in this area was not increased in the highly motivated non-depleted participants as compared to the regularly motivated participants. Thus, based

on very similar reasoning as against the process model, the opportunity cost model is unable to explain our findings.

The labor/leisure tradeoff model suggests that activity in lateral prefrontal areas, especially the IFG, is related to effort and the subjective experience of task costs. The particularly strong IFG in highly motivated, depleted participants suggests that they invested extra effort in the task, and thus should experience higher subjective costs than participants in the other conditions. This is perfectly in agreement with our own interpretation. Yet similar to the process model and the opportunity cost model, the labor/leisure tradeoff model cannot give an adequate explanation why highly motivated, depleted participants should invest greater effort, inducing even stronger aversive experiences of costs, then all other participants.

Different from the opportunity cost model and the labor/leisure tradeoff model, the resource allocation model (Beedie & Lane, 2012) did not exclude the resource concept from their model, but argued the problem lies in allocating the resource, not in its supply. This model is practically indistinguishable from the strength model, which adopted this view in its most recent overhaul (Baumeister, 2014). It might be that the increased IFG activity in highly motivated depleted participants is related to allocating additional resources to this area. This possibility will be discussed in more detail in chapter 3.3.

Three other brain imaging studies reported that depletion induced changes in IFG functioning (Friese et al., 2013; Persson et al., 2013; Wagner et al., 2013). Thus IFG, which takes a central role in inhibition (e.g. Nee et al., 2007), is the most consistently reported area for depletion effects. One other study reported depletion-related increases in prefrontal areas. Specifically, Persson et al. (2013) found that depletion decreased activity in left prefrontal areas, but increased activity in similar right prefrontal areas. It cannot be ruled out that the right-lateralized increase might be part of the neural expression of self-

control exertion effects. Yet in light of other studies only reporting decreases after self-control exertion (e.g. Friese et al., 2013; Hedgcock, Vohs, & Rao, 2012), it seems unlikely that activity increases are responsible for depletion effects. Alternatively, Persson et al. (2013) suggest it might be a compensatory mechanism by which depleted participants try to make up for the loss of left-hemisphere resources. In our study, we found that motivation lead to a direct compensatory effect in the brain area which otherwise decreased its activity after self-control exertion. An important difference between these two findings is that the motivated group in our study was able to overcome depletion-related impairments in performance, while Persson et al.'s (2013) sample of "regularly motivated", depleted participants showed the usual performance impairments. Activating contralateral areas might be a less-effortful strategy, which has some beneficial effects for performance, but cannot fully compensate for the depletion effects. Similar effects can be observed after a brain stroke, when patients learn to use different or contralateral areas in tasks which normally rely on stroke-affected areas. While this compensation is beneficial, it is still accompanied by performance impairments. On the contrary in our study, boosting motivation in depleted participants might have pushed them to adopt a more effortful, but more effective strategy to overcome self-control exertion – which was to increase activity in an area most specialized for the task at hand and itself affected by self-control exertion.

In sum, our findings are difficult to reconcile with a purely motivational account of self-control. Highly motivated, depleted participants had to compensate for something which did not instantly replenish with a motivational boost. The best explanation remains that these participants had to overcome a partial depletion of self-control resources. In line with the resource conservation principle, depletion made participants less willing to spend more self-control resources, but they could do so if they were sufficiently motivated. Integrating concepts from the labor/leisure tradeoff model, one may reason that

individuals are motivated to conserve the resource because engaging in self-control becomes subjectively more costly when less of the resource is available.

Second study: Lingering effects of depletion on the human brain at rest

Brain activity during emotion suppression was in expected areas, but unusually weak in comparison to meta-analytic findings (Buhle et al., 2014; Diekhof et al., 2011; Frank et al., 2014; Kohn et al., 2014). Prefrontal areas did not survive correction for multiple comparisons, even if small-volume correction was applied to the area of interest, the IFG. One might wonder if effects on the subsequent resting state would have been stronger or different, had we found stronger emotion suppression activation. Cautionary words are also appropriate in relation to the finding of altered connectivity between the IFG and the OFC. The affected cluster in the OFC lies in its most anterior part, directly inferior to the frontal pole. This area is very exposed in the sense that it is encompassed by a lot of non-brain tissue. Small movements can cause the same voxels in this area to measure varying proportions of brain and non-brain tissue, which leads to signal fluctuations of a much higher magnitude than the BOLD effect. The OFC is not traditionally associated with emotion suppression or other regulatory processes and we cannot exclude the possibility that the presumed connectivity changes might be due to motion artifacts, even after the application of methods to correct for movement.

Our findings are somewhat at odds with a study by Wagner and Heatherton (2013), which reported that prior self-control exertion led to decreased connectivity between the ventromedial prefrontal cortex and the amygdala during an emotional picture task. Different from our study, this was a psychophysiological interaction analysis during the task, the emotional picture task served as dependent second task, and there was no instruction to suppress emotional responses. On the one hand, under the assumption that

connectivity changes during rest reflect previous task-related activity, it is surprising that we found no connectivity changes related to the ventromedial prefrontal cortex or the amygdala. On the other hand, the study from Wagner and Heatherton (2013) can be criticized on multiple grounds (see chapter 2.3 and the next section), and our finding of increased connectivity related to the IFG is in line with the majority of neuroscientific depletion studies (Friese et al., 2013; Luethi, Friese, Binder, et al., submitted; Persson et al., 2013; Wagner et al., 2013).

Third study: Self-control exertion and emotion regulation

The fundamental question for our study is why we were not able to replicate the findings from Wagner and Heatherton (2013). We have described statistical concerns about their methods in the manuscript (chapter 2.3) and concluded that changes in amygdala activity might not be a reliable consequence of depletion. Here I will explore other potential explanations for the differing findings which concern the way emotion regulation and self-control interact. Because we found no self-control exertion effects on emotional processing, it is consequential that emotional memory performance was not affected as well. Thus I will not discuss these results again.

In retrospect, the potentially biggest flaw in the study design is that we do not know if the participants engaged in emotion regulation at all, and if they did so, how much effort they invested into emotion regulation and what emotion regulation strategies they used. This issue becomes even more pressing in consideration of a recent study by Wang et al. (2014), which suggested that suppression, but not reappraisal, demands effort and induces self-control exertion. This finding integrates well with general comparisons of emotion regulation strategies. Overall, reappraisal seems to be a more successful strategy

to regulate emotions than suppression in terms of affective, cognitive, and social outcomes. Reappraisal decreases the emotional experience to a larger degree than suppression (Gross, 2002). On the other hand, suppression, but not reappraisal, increases sympathetic activation above baseline, as indicated by electrodermal activity and the cardiovascular system (Gross, 2002; Richards, 2004). This increase has been interpreted to reflect the greater cognitive costs of suppression. Suppression, especially concealing outwards signs of emotions, needs constant monitoring and correction throughout an emotional experience. By contrast, reappraisal is evoked earlier in the emotion generation process and requires less continual self-regulatory effort during an emotional event. Furthermore, it has been shown that suppression, but no reappraisal, impairs subsequent memory. Relying on the concept of limited parallel computational capacities (e.g. Kurzban et al., 2013), this may indicate that suppression demands more computational mechanisms than reappraisal, which could otherwise support successful memory encoding. Other emotion regulation strategies exist (see chapter 1.5), though they have been studied less. Like reappraisal, they are antecedent-focused, hence one could speculate that they are less effortful than suppression. Critically, only suppression refers to inhibition of an emotional response, which makes it more similar to the core component of self-control and thus more likely to depend on the same limited resource as self-control, than other emotion regulation strategies.

Wagner & Heatherton (2013) reported a weakened connectivity between the amygdala and the VMPFC after depletion. The authors argue that the VMPFC is an area commonly associated with emotion regulation. Only one meta-analysis out of four reported activity in the VMPFC (Diekhof et al., 2011). A closer inspection revealed that the activity in the VMPFC originated from three studies only. Two of these used an emotion regulation instruction which mixed reappraisal and suppression (Johnstone et al., 2007;

Urry et al., 2006). In the third study, participants were instructed to reappraise, but stimuli were fear-conditioned with electric shocks (Delgado, Nearing, LeDoux, & Phelps, 2008). One could argue that enduring electric shocks involves suppression in addition to reappraisal in order to cope with the pain. In sum, while the VMPFC does not seem to be a central area of emotion regulation, it may be that this area has a more specific role in emotion suppression. However, caution is necessary when comparing these meta-analyses to spontaneous emotion regulation as in the study by Wagner and Heatherton (2013). Typical emotion regulation studies, which are the main bulk of these meta-analyses, compare emotional pictures with the instruction to regulate emotion to neutral or emotional pictures with no instruction to regulate. Wagner and Heatherton (2013) and our study compared emotional pictures to neutral pictures. Thus we cannot exclude the possibility that VMPFC activity is related to the differences in contrasts. For example, it could be that the VMPFC is activated when participants are spontaneously engaging in emotion regulation, as compared to being explicitly told to do so.

Regarding our own study, we also found that depletion reduced activity in the VMPFC. This might be interpreted as evidence that there is a depletion effect, but it had no consequences for emotion regulation, as participants chose other emotion regulation strategies which did not involve the VMPFC. There are two critical remarks to this interpretation. First, in order to show depletion-induced decreases, the VMPFC must have shown some level of activity prior to depletion. This may suggest that participants used suppression to regulate emotions prior to self-control exertion, but switched to other emotion regulation strategies not dependent on the VMPFC when depleted. While this is theoretically possible, it is highly speculative. Second, our finding, even though part of the VMPFC, lies superior to the one reported by Wagner and Heatherton (2013). Anatomical connections between the amygdala and the VMPFC are highest in its inferior and caudal

sections, which are closer to the amygdala (Ghashghaei, Hilgetag, & Barbas, 2007). This renders it somewhat less likely that the area of VMPFC where we found depletion-induced activity changes is directly involved in emotion regulation. In face of these critical remarks, our VMPFC finding is puzzling. One may add that the activity changes were relatively weak and did not survive appropriate correction for multiple comparisons.

Conclusively, it might be that the participants in Wagner and Heatherton's (2013) study regulated emotions primarily by suppression, whereas the participants in our study engaged more often in less demanding emotion regulation strategies, such as reappraisal. This possibility seems to be in line with cultural differences in the habitual use of emotion regulation strategies. A cross-cultural study revealed that Swiss citizens as compared to citizens of the USA make relatively more habitual use of reappraisal than suppression to regulate emotions (Matsumoto, Yoo, & Nakagawa, 2008). Unfortunately, neither Wagner and Heatherton (2013) nor we have assessed what emotion regulation strategies the participants pursued and thus any conclusions remain highly speculative. Another possibility is that the usage of two self-control exertion tasks in our study induced lower levels of self-control exertion than one self-control task. This seems counter-intuitive, yet there is some evidence for this effect (Carter et al., 2015). In any case, research on self-control (Wang et al., 2014) and emotion regulation (Gross, 2002; Richards, 2004) suggest that it is specifically emotion suppression which is costly and thus susceptible to self-control exertion manipulations. Future research examining self-control and emotion regulation interactions would profit from an explicit instruction to suppress emotional responses.

3.2 An integrative neuroscientific perspective on depletion

This chapter will focus on two things. First, mainly based on fMRI studies, I will circumscribe which brain areas are critically involved in self-control exertion effects. Second, I will review what neurophysiological findings might tell us about a possible physical basis of the self-control resource. Table 1 provides an overview of all brain areas which have been found to reduce functioning after depletion. All seven studies reported changes in prefrontal areas. The most reported finding was reduced activity in lateral prefrontal areas after self-control exertion (see Fig. 3 for an overview of these papers). These areas has been identified as a key structure for cognitive and emotional control (chapters 1.3 & 1.5). This supports the view that self-control fails because of a breakdown of top-down control (Heatherton & Wagner, 2011).

A closer look reveals that the brain area of depletion-induced reduction can be related to the second task. Hedgcock et al. (2012) used a choice task where participants chose between indulgent and healthy snacks. The primary aspect of exerting self-control in this context might be to weigh the different options against each other and select the one which is in line with long-term goals. These mental operations are associated with the MFG, which was the area with reduced activity after self-control exertion in Hedgcock et al.'s (2012) study. In Persson et al.'s (2013) experiment, participants had to generate a verb associated with a presented noun. Verb selection is not related to goals and thus quick task processing might be more dependent on inhibiting alternatives once an answer has come to mind. Accordingly, depletion reduced activity in the IFG. Furthermore, in line with the task's heavy reliance on language, this activity change was in the left hemisphere. Two studies used the Stroop task as their second task (Friese et al., 2013; Luethi, Friese, Binder, et al., submitted). The Stroop task is cognitively very demanding and it has been argued that correct task processing relies both on response selection and inhibition.

Hence activity occurs bilaterally in the MFG and IFG (Nee et al., 2007). Indeed, Friese et al. (2013) found decreased activity in the right MFG and IFG after depletion. In our study (Luethi, Friese, Binder, et al., submitted), activity changes only occurred in the left IFG, but given the verbal nature of the task, this is a very critical area for task processing. Wagner et al. (2013) also reported changes in the IFG after depletion, yet not activity reductions but decreased connectivity with the OFC. During the second task, dieters watched tempting food items, but did not have to respond to them. Thus the IFG was probably involved in inhibiting the craving for food induced by the pictures. Finally, two studies, where the second task was related to emotional processing, showed changes in the VMPFC (Luethi, Friese, Binder, et al., submitted; Wagner & Heatherton, 2013).

Based on this rather small sample of studies, it is not clear if the first task contributes to the exact area of depletion-induced activity changes. Persson et al. (2013) conducted a conjunction analysis where they could reveal that the IFG was the only area which was significantly activated by both tasks. While it was not a perfect overlap, the cluster identified was very close to the one showing depletion effects. This suggests that resource depletion occurs in brain areas which are heavily involved in both tasks. Unfortunately, the other studies did not report brain activity from the first task. In our own studies, we either found no depletion effects (Luethi, Friese, Schroeder, et al., submitted) or no activity during the first task (Luethi, Friese, Binder, et al., submitted). In the latter case, this was probably due to a power problem. Participants had to suppress thoughts during blocks of 60 s in the first task. Blocks with a longer duration than approximately 20 s become increasingly less likely to detect signal changes because of necessary high-pass filtering of the brain signal (Amaro & Barker, 2006).

Table 1
Brain areas with reduced functioning after depletion.

						MNI coordinates				
Study	Authors	Area	R/L	BA	Cluster size	*x*	*y*	*Z*	Task 1	Task 2
1	Hedgcock et al. (2012)	Middle frontal gyrus	R	9/44	1180	40	26	36	Attention-control task	Choice task
2	Friese et al. (2013)	Middle & inferior frontal gyrus	R	9/45/48	22	50	22	28	Emotion suppression	Stroop task
3	Persson et al. (2013)	inferior frontal gyrus	L	46	-	-40	26	2	Working memory task	Verb generation
	Persson et al. (2013)	anterior cingulate cortex	L	24	-	-8	22	28		
	Persson et al. (2013)	Striatum	L		-	-8	4	-4		
4	Wagner et al. (2013)	inferior frontal gyrus	L & R	48		±45	24	18	Attention-control task	Watch food pictures
5	Luethi et al. (submitted)	inferior frontal gyrus	L	45	108	-36	38	12	Thought-suppression task	Stroop task
6	Wagner & Heatherton (2013)	Ventromedial prefrontal cortex	L	11	-	-12	54	-15	Attention-control task	Watch emotional pictures
7	Luethi et al. (submitted)	Ventromedial prefrontal cortex	L	10	20	-12	60	4	Stroop & thought-suppression task	Watch emotional pictures

Note. This table lists brain areas possibly implicated in control which reduced activity after self-control exertion in all available fMRI studies on this matter. Exceptions are the two studies by Wagner and Heatherton (2013) and Wagner et al. (2013), where the specified areas showed decreased connectivity (not activity) with brain areas implicated in emotion processing (amygdala, orbitofrontal cortex). Persson et al. (2013) were the only ones to report more than one region. One additional finding in the cerebellum has been omitted for this table. Not shown are areas which increased activity after self-control exertion. Cluster size is indicated if this information was provided. R, right; L, left; BA, Brodmann area.

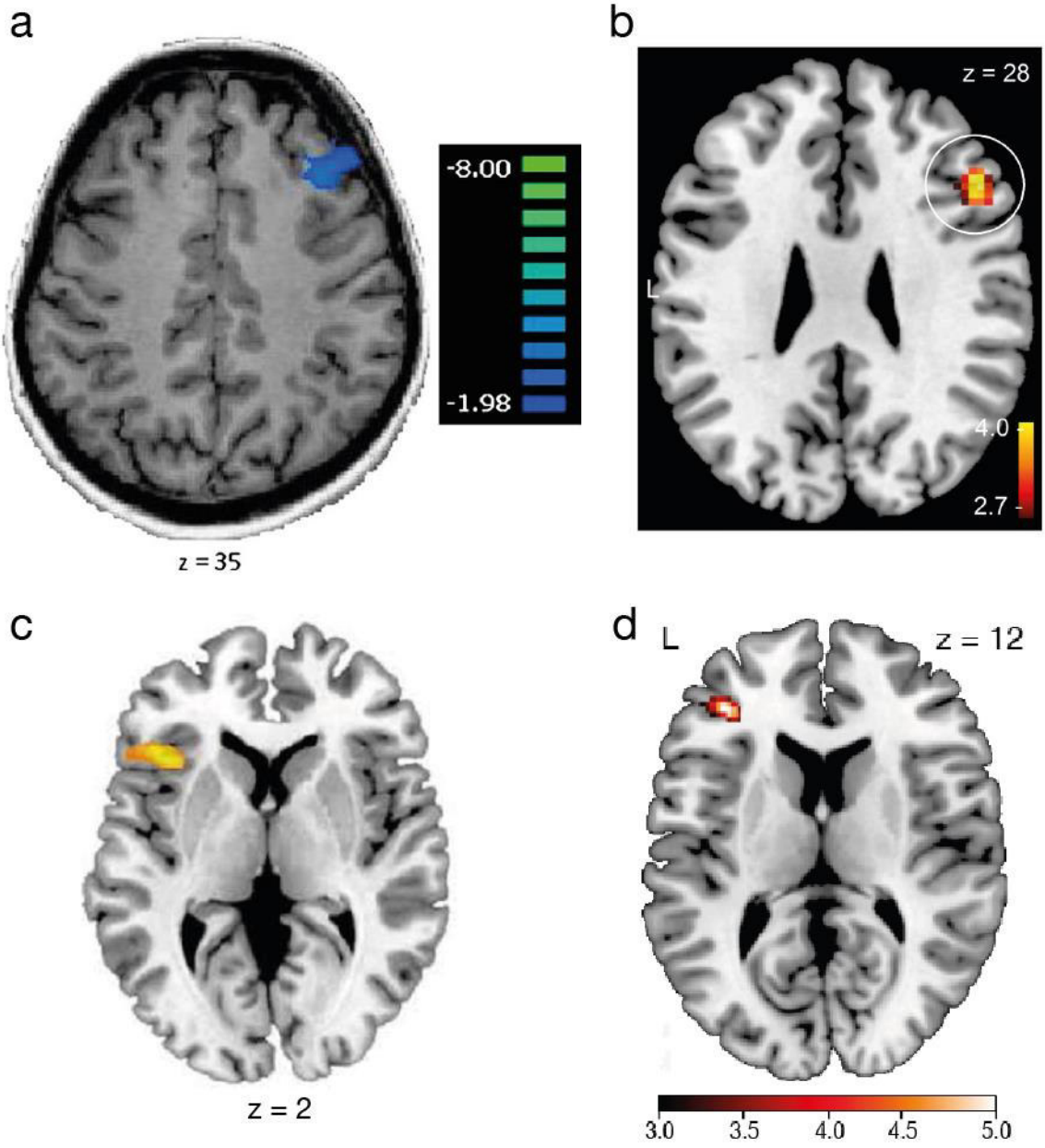

Fig. 3. Findings of reduced lateral prefrontal activity after self-control exertion. (a) Retrieved from "Reducing self-control depletion effects through enhanced sensitivity to implementation: Evidence from fMRI and behavioral studies" by W. M. Hedgcock, K. D. Vohs, & A. R. Rao, 2012, *Journal of Consumer Psychology,* 22, p. 489. (b) Retrieved from "Suppressing emotions impairs subsequent Stroop performance and reduces prefrontal brain activation" by M. Friese, J. Binder, R. Luechinger, P. Boesiger, & B. Rasch, 2013, *PLOS ONE,* 8, p. 7. (c) Retrieved from "Imaging fatigue of interference control reveals the neural basis of executive resource depletion" by J. Persson, A. Larsson, & P. A. Reuter-Lorenz, 2013, *Journal of Cognitive Neuroscience,* 25, p. 346. These authors did not provide a scale for the figure. (d) Retrieved from our second publication manuscript.¨

While the exact location of depletion effects varies, the studies consistently reported changes in functionality within a domain-general network of cognitive control. Hence, these findings also support a general domain of self-control, which is one of the central assumptions of the strength model (e.g. Baumeister et al., 2007). The most frequent finding was that the IFG showed reduced functioning after depletion. This area has been associated with inhibition in general (Aron et al., 2014; Aron, 2007; but see Swick & Chatham, 2014, for a different view). Others have shown that activity in the IFG overlaps during various acts of self-control (Tabibnia et al., 2014). Besides the IFG, fMRI studies found depletion-induced activity decreases in the MFG, which has been associated with response selection (Nee et al., 2007). In the two-stage model of self-control (Myrseth & Fishbach, 2009), inhibition and response selection are summarized as the implementation stage of self-control. The other, earlier stage is recognizing the need for self-control, which is anatomically linked to the ACC. Friese et al. (2013) specifically tested for depletion-induced changes in the ACC (which is associated with monitoring), but found no effects. Only Persson et al. (2013) reported that depletion decreased activity in the ACC, in addition to decreases in the IFG. These studies in concert suggest that depletion impairs primarily the implementation stage of self-control. However, two EEG studies led to different conclusions (Inzlicht & Gutsell, 2007; Wang et al., 2014). They reported depletion induced changes in the error-related negativity (ERN), a part of the event-related potential associated with error monitoring and the ACC (Van Veen & Carter, 2002; Van Veen & Miller, 2007). The comparability of the opposing findings is hampered by the fact that they stem from different methods, and that fMRI models are based on correct trials, whereas the ERN follows error trials. Yet EEG does not provide the means to clearly locate the measured signal and it cannot be excluded that lateral prefrontal areas play a (minor) role in the generation of the ERN besides the ACC. It is at least very likely that prefrontal areas

were less activated during error trials than during correct trials. In sum, for the time being, we cannot exclude the possibility that depletion affects conflict monitoring in addition to self-control implementation. Further research is definitively warranted. Potentially a combined EEG/fMRI depletion study might reveal new insights into this matter.

A final question is how the VMPFC finding can be integrated into the neural framework of depletion provided by the other studies. This area does not form part of a domain-general control network. As discussed previously, this finding stems from one study (Wagner & Heatherton, 2013), but we were unable to reproduce it and have questioned these results on statistical grounds (chapter 2.2). Most meta-analyses report that areas involved in emotion regulation highly overlap with the cognitive control network (Buhle et al., 2014; Frank et al., 2014; Webb, Miles, & Sheeran, 2012). Nevertheless, it could be that the VMPFC takes a more down-stream role in emotion suppression which is ultimately controlled by lateral prefrontal areas. This assumption is accordance with anatomical research reporting that direct connections between lateral prefrontal areas and the amygdala are fewer than between the VMPFC and the amygdala (Ghashghaei et al., 2007).

In conclusion, depletion effects seem to mainly relate to prefrontal areas which are also critically involved in cognitive control, especially the IFG. This supports the notion of the domain-generality of self-control. In addition, depletion seems more likely to affect the lateral prefrontal areas implicated in the implementation of self-control than the ACC implicated in conflict detection.

Next I will give an overview of potential neurophysiological bases for the self-control resource. Baumeister (2014) recently defended the notion that glucose is the physiological basis for the limited self-control resource, yet left it unclear how this relates to neurophysiological processes. Kurzban (2010) has challenged this assumption to be highly implausible based on neurophysiological work. He cited work from Raichle and

Mintun (2006) which concluded that local energy usage rises no more than a few percent when task demands increase. In a next step, Kurzban (2010) incorrectly assumed that energy expenditure is synonymous with glucose consumption. However, Raichle and Mintun (2006) also cited their earlier work which showed that increases in local blood flow in response to increased task demands led to increases in glucose uptake by as much as 51% (P. T. Fox, Raichle, Mintun, & Dence, 1988). In other words, increases of local glucose usage are proven to be around 50 times higher than what Kurzban (2010) assumed. The difference between energy consumption and glucose uptake derives from the fact that local oxygen uptake only changes very little. Oxygen is used in combination with glucose for efficient energy production, whereas consumption of glucose without oxygen (anaerobic glycolysis) is highly inefficient. Nevertheless, it remains highly implausible that a measureable effect in the blood glucose levels would appear. Yet one could interpret this finding as evidence for the resource allocation hypothesis. Local blood flow is increased in response to increased neural activity levels, allowing allocating additional glucose to this area. While this possibility cannot be excluded, it is not what Raichle and Mintun (2006) inferred. They pointed out that neural tissue has stored abundant amounts of glucose (and glycogen), making adequate reserves available in times of higher need. They conclude that usage of additional glucose (or oxygen) cannot be responsible for the increases in local blood flow, and that the function of this phenomenon is unknown. They suggest that "one might consider the possibility that it [=increase in local blood flow] is used for the removal of the excess lactate produced [as a byproduct of anaerobic glycolysis] during an increase in activity or the adjustment of the acid-base or ionic balance of the tissue. Likewise, temperature regulation, a long-overlooked subject, may be playing some role." (Raichle & Mintun, 2006, p. 468). It could be that any of these physiological

factors form the base for the self-control resource, though this is highly speculative. Another idea is that local availability of neurotransmitters might decrease after a period of increased activity, potentially having a negative impact on synaptic efficacy (Brzezicka, Kaminski, & Wróbelb, 2013). Critically, it is difficult to explain why this resource problem should be specific to self-control and not be related to all kinds of neural information processing, such as input in the visual system. In summary, no conclusion can be drawn with respect to the neurophysiological basis of the self-control resource.

3.3 Difficulties replicating depletion

During my PhD project, I encountered problems to replicate depletion effects. One fMRI study failed to find evidence for depletion, and another pilot study was unsuccessful at inducing depletion effects as well. Furthermore, I have been involved in a collaborative project where we looked at potential depletion effects in three study samples where participants engaged in a series of working memory tasks, including Stroop and Flanker tasks, over a period of two hours or more (De Simoni, Luethi, & Von Bastian, in preparation). According to the study from Vohs et al. (2013) and our general understanding of the strength model, we assumed that severe levels of depletion should occur over the course of the tasks. In two studies, there was no effect and in the third, participants became better at tasks if they had engaged in other tasks previously. In sum, only two out of five study projects I have been involved in showed self-control exertion effects, and one (first study) demonstrated the expected drop in performance (while the other measured effects on resting state connectivity, second study). In this chapter, I will first list factors which possibly complicate the transition from social-psychological, behavioral studies to

fMRI. Then I will discuss the very recent meta-analytic debate about the reliability of depletion effects.

Regarding the transition to fMRI, a first complicating factor is that some tasks cannot be used or would be very difficult to adapt for an fMRI study. Frequently used example tasks are anagrams, handgrip, crossing out letters (Hagger et al., 2010). This often leads to a more cognitive focus in fMRI tasks. Secondly, fMRI tasks have to be longer than the average behavioral depletion task. In order to achieve a satisfactory signal-to-noise ratio for the brain signal, a trial has to be repeated 20 times at the minimum. Thirdly, fMRI studies must rely on computerized versions of tasks which is usually not the case in social-psychological experiments. It could be that the socially more interactive nature of behavioral experiments somehow contributes to depletion effects. Fourthly, fMRI scanning requires participants to lay as still as possible in order to measure an undistorted brain signal. They must inhibit any movements, which could already induce some amount of depletion in all participants, which increases with longer scanning duration. Fifthly, in many participants, the hospital setting and the knowledge of having their brains scanned creates excitement and thus they might be more motivated than in a behavioral study. Furthermore, at least in Switzerland, participants are much better paid for fMRI studies, as they have to receive CHF 25 per hour by law. In behavioral studies, individuals often participate for course credit or for a payment of CHF 15 per hour or less. These two factors might motivate participants to invest more effort in fMRI studies, which could possibly counteract depletion effects.

In light of the difficulties to reproduce depletion effects, one might also wonder about the overall reliability of depletion effects. The commonly known meta-analysis was conducted by Hagger et al. (2010) and led them to conclude that “the strength model is a useful explanatory system with which to understand self-control” (p. 520) and that the

results "corroborate the view that self-control draws from a single, global resource and depletion is not an artifact of specific spheres and tasks" (p. 515). Yet, more recently Carter and McCullough (Carter et al., 2015; Carter & McCullough, 2013, 2014) conducted several meta-analytic tests and reported that they "found only scant evidence that the depletion effect is distinguishable from zero" (p. 796, 2015), and that "the meta-analytic evidence does not support the proposition (and popular belief) that self-control functions as if it relies on a limited resource" (p. 813, 2015). How can it be that meta-analyses examining the same effect arrive at opposing conclusions? In short, Carter et al. (2013, 2014, 2015) make two major claims why Hagger et al.'s (2010) analysis is flawed. One, Hagger et al. (2010) did not take adequate steps to test and correct for publication bias. Two, some of the experiments in the meta-analysis by Hagger et al. (2015) did not measure self-control directly. Carter et al.'s (2014, 2015) crushing verdict is based on a reanalysis of Hagger et al.'s (2010) original data as well as a recently published new meta-analysis on depletion effects. They independently searched for published and unpublished depletion studies and only included experiments with frequently used tasks in the analysis, which also led to a restriction to studies that tested the core depletion effect. The publication from Carter et al., (2014, 2015) has resulted in immediate reactions and attempts to rebut their meta-analytic techniques (Gervais, 2015; Hagger & Chatzisarantis, 2014; Inzlicht, Gervais, & Berkman, 2015). Most recently, Inzlicht et al. (2015) agree that meta-analyses on depletion should be bias-corrected, yet they suggest that Carter et al.'s (2015) "correction attempts might themselves be in need of correction." (p.13). Based on further meta-analytic tests, Inzlicht et al. (2015) reported a moderate depletion effect and stated that "[at] the very least, concluding that the ego depletion effect is zero based on these techniques is premature" (p. 13). In light of these widely different conclusions, the question remains which is the more accurate interpretation of the empirical findings. In order

to be able to judge for oneself, a more detailed and critical look at the meta-analyses is necessary. I will continue this chapter with a comparison of the reported effect sizes, how publication bias was estimated, and what steps were taken to correct for it. Following the claim from Inzlicht et al. (2015) that sample sizes become too small for meta-analytic tests when studies are split into different depletion subdomains, I will restrict reporting to the estimation of the overall depletion effect size.

Meta-analytic effect sizes of depletion. As reported in the introduction, Hagger et al. (2010) found an overall medium-to-large effect size $d = 0.62$ (Confidence Interval [0.57, 0.67]), which was verified by Carter and McCullough (2014). In Carter et al.'s new meta-analysis, a reduced overall effect size was reported of $d = 0.43$ (Confidence Interval [0.34, 0.52]), equal to a small-to-medium effect. This difference arises from the different study inclusion criteria outlined above. Inzlicht et al. (2015) state that Carter et al.'s (2015) new sample is an improvement over the one from Hagger et al. (2010), providing a better foundation to estimate the true depletion effect.

Estimation of publication bias. Any meta-analysis might be biased to the extent that the underlying sample of experiments misrepresents the population of all experiments conducted on a particular effect. The main concern is that studies with significant outcomes are more likely to be submitted and accepted for publication than studies without significant outcomes. This phenomenon is known as publication bias or file-drawer symptom. Finding signs of publication bias is very common when conducting meta-analyses (Ferguson & Brannick, 2012). Hagger et al. evaluated this possibility by calculating the

fail-safe *N*[1] (Rosenberg, 2005), a frequently used method to deal with publication biases in psychological science (Carter & McCullough, 2014). This method suggested the findings stand robustly against a potential bias. However, the fail-safe *N* has been widely criticized for relying on unrealistic assumptions and statisticians recommended against its use (Ferguson & Brannick, 2012; J. P. A. Ioannidis, 2008). Other estimations uniformly indicated evidence for the presence of a bias in both depletion datasets (Test for Excess Statistical Significance, Trim and Fill, meta-regression models). Furthermore, the presence of a bias can be diagnosed by visual inspection of funnel plots[2]. Figure 3 presents a funnel

[1] The fail-safe *N* estimates the number of unpublished experiments with an average effect of zero that would have to exist in order to bring the meta-analytically calculated effect size down to zero. Hagger et al. (2010) found this would have to be 50'445 unpublished, insignificant experiments. Understandably, Hagger et al. (2010) concluded it is highly unlikely that such a big number of unpublished depletion studies existed.

[2] Funnel plots compare the standard errors of effect sizes against the magnitude of the effect sizes. Standard errors provide an estimation of the random error and thus of the achieved measurement precision. Every time an effect is measured, it is affected by a random error, which causes study outcomes to fluctuate around the true effect, sometimes underestimating, sometimes overestimating its magnitude. Random errors are heavily influenced by study size: The outcomes of larger studies are expected to lie closer to the true effect size, whereas smaller studies are less precise and their outcomes are more scattered. A publication bias prevents smaller studies with smaller effects from getting published, while smaller studies with overly large effects appear more often in published studies. This results in an asymmetrical distribution of studies. In some cases, such asymmetry might be caused by other reasons than a publication bias, thus they are collectively referred to as "small-study effects". For example, in treatment studies it is often the case that smaller (pilot) studies are conducted with high-risk patients that profit more from treatment than patients in larger samples. For depletion studies however, the most plausible cause for a small-study effect is a publication bias.

plot for all studies included in the meta-analysis by Hagger et al. (2010) and strongly suggests the presence of a publication bias. Inzlicht et al. (2015) again agree with Carter et al. (2013, 2014, 2015) that correction for publication bias should be applied.

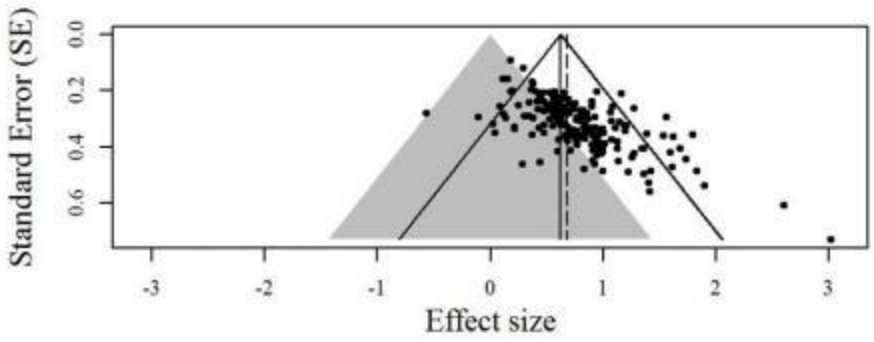

Fig. 4. Contour-enhanced funnel plot of published depletion studies. Studies should scatter into a symmetrical funnel shape. When studies are highly precise (mainly due to big sample sizes), the standard error will be small and outcomes will cluster tightly around the true effect size (top end of funnel). When studies are less precise (mainly due to small sample sizes), outcomes will deviate more to the left and right of the true effect size (bottom end of funnel). The grey area represents the expected distribution under the assumption of a null effect. Effect sizes that fall within this area are non-significant. The solid/dashed vertical line represents the estimate for the overall effect from a fixed-effect/random-effects model. The solid angled lines represent the bounds within which 95% of the studies should fall, given the estimated effect size. If there was no publication bias, studies would fall equally and symmetrically to the left and right of the estimated effect size, within the funnel indicated by the solid lines. Instead, measurements are asymmetrically distributed, such that studies with a higher standard error consistently show a higher effect than studies with a lower standard error. Retrieved from "Publication bias and the limited strength model of self-control: Has the evidence for ego depletion been overestimated?" by E. Carter and M. McCullough, 2014, *Frontiers in Psychology,* 5, p. 7.

Correcting for publication bias. Different ways to correct the estimated effect size for a publication bias exist, which are the trim-and-fill method (Duval & Tweedie, 2000), meta-regression models based on PET-PEESE (Egger, Smith, Schneider, & Minder, 1997;

Moreno et al., 2009), the *p*-curve estimate (Simonsohn, Nelson, & Simmons, 2014), or restriction to the top-10 studies with the highest sample size (Stanley, Jarrell, & Doucouliagos, 2010). The trim-and-fill method re-estimated a small or medium effect size, depending on the dataset (Hagger et al.'s (2010) dataset: g = 0.48, Confidence Interval [0.44, 0.51]); Carter et al.'s (2015) dataset: g = 0.24, Confidence Interval [0.13, 0.34]). Even though the trim-and-fill method is more commonly used in psychological science, statisticians argue that it tends to under-correct for publication bias (Moreno et al., 2009; Rücker, Carpenter, & Schwarzer, 2011). For meta-regression models, there are two different implementations: the Precision Effect Test (PET) and the Precision Effect Estimate with Standard Error (PEESE). Carter et al. (2014, 2015) have used them inconsistently over their two meta-analyses in order to show that depletion effects are always indistinguishable from zero. While PET arrives at strongly negative effect sizes in some cases, I would argue that PEESE might produce more probable corrections. PEESE indicates either a small depletion effect (based on Hagger et al.'s (2010) dataset: g = 0.25, Confidence Interval [0.18, 0.32]) or a zero effect (based on Carter et al.'s (2015) dataset: g = 0.01, Confidence Interval [-0.14, 0.15]). While Carter et al. (2015) argue that meta-regression models fare better than other techniques on simulated and real data, Gervais (2015) amply demonstrated on simulated data that meta-regression models consistently underestimate the underlying effect if it is heterogeneous, which is highly plausible for depletion effects. With simulations aiming at realistic conditions resembling the depletion research, meta-regression models distorted the effect size by over 50%, often returning null effects even when there was a true effect (Inzlicht et al., 2015). Instead, Inzlicht et al. (2015) introduce the *p*-curve estimate, which showed an acceptable performance in their simulations. Applied solely to Carter et al.'s (2015) dataset, p-curves indicated a medium depletion effect size (g = 0.55, Confidence Interval [0.45, 0.59]). Like meta-regression

methods, the *p*-curve estimate is a fairly new technique, which has seen little application so far. It is odd that the *p*-curve estimate returns a corrected effect size that is larger than the original uncorrected effect size. This technique was specifically developed to correct for bias without requiring access to nonsignificant results, yet Inzlicht et al. (2015) applied it to Carter et al.'s (2015) dataset, which contained unpublished and nonsignificant results. Finally, the estimate derived from the top-10 studies with the highest sample size was also applied to Carter et al.'s (2015) dataset, which returned a small effect size (g = 0.26, Confidence Interval [0.07, 0.44]; Inzlicht et al., 2015).

It seems that meta-analyses, with a plethora of techniques to choose from, are far from objective tools to estimate effect sizes in an unbiased way. The majority of tests and visual inspection of the data indicate that a correction for publication bias is warranted. In agreement with Carter et al. (2015) and Inzlicht et al. (2015), Carter et al.'s (2015) dataset might provide a more suitable basis to estimate the true depletion effect size. Similar to Inzlicht et al. (2015), I suggest it is advisable to consider a range of effect sizes which are all possible, as ordered by magnitude: (*a*) the estimate derived from the *p*-curve (g = 0.55), (*b*) the uncorrected estimate from Carter et al. (2015), which consists of 41% unpublished studies (g = 0.43), (*c*) the estimate derived from the top-10 studies (g = 0.26), (*d*) the trim-and-fill derived estimate (g = 0.24), and (*e*) the estimate derived from PEESE (g = 0). In conclusion, the true depletion effect has most likely a magnitude between zero and medium (g = 0.55). Based on the most favorable circumstances, the *p*-curve estimation, 53 participants per group are required to achieve 80% power to detect a depletion effect. According to the trim-and-fill correction method, which is a fairly established technique and its estimation lies in the middle of other estimates, this number rises to 274 participants per group. While these numbers are above realistic sample sizes in fMRI-studies, also behavioral scientists measured less participants in most studies (median *N*

= 48; Carter et al., 2015). Therefore, overall statistical power was low, and one may wonder why there were so many significant findings at all. When looking at the funnel plot (Fig. 4), one can notice a big cluster of studies lying directly to the right of the grey area, thus just below the significance threshold. One may speculate that at least part of these results stem from researchers turning less favorable findings into favorable ones, e.g. by statistical adjustments, restricting reporting only to significant outcome variables and/or statistical tests with significant outcomes. These and other questionable research practices are believed to be fairly common in all fields of psychology (John, Loewenstein, & Prelec, 2012; Simmons et al., 2011). Altogether, the analyses and considerations suggest that there is reason to adopt a critical attitude towards the current depletion research.

3.4 Future research questions

With regard to the controversial meta-analytic findings (Carter et al., 2015; Carter & McCullough, 2013, 2014; Hagger et al., 2010; Inzlicht et al., 2015), future research should focus on examining the reliability of depletion effects. All researchers involved have recommended that large, pre-registered direct replications of depletion studies should be conducted. In fact, Holcombe and Hagger have already initiated such a project (see https://osf.io/jymhe/).

If replication projects are able to reproduce depletion effects, several interesting study lines exist. Here I will list open questions in depletion research and finally provide a more detailed description of a study outline which would integrate several new approaches to examine depletion. First, one could re-examine interactions between depletion, emotion regulation, and emotional memory formation. This would essentially be the

same study as our third study (chapter 2.3), but participants should be explicitly instructed to suppress emotional reactions. Secondly, magnetic resonance spectroscopy (MRS) might allow new insights into the physical basis of the self-control resource. MRS measures concentration of various neurometabolites in a circumscribed area of the brain. Based on our review of neuroscientific depletion studies, such an approach could focus on the IFG. Thirdly, from the perspective of research on cognitive control, the depletion literature has unnecessarily restricted itself to a handful of tasks. For example, one could also examine depletion effects with the Simon task, the Flanker task, the stimulus-response compatibility task, the Stop-signal task, or the Go/go-no task. Especially the Stop-signal task is in theory ideally suited to study depletion, as correct task processing is highly dependent on inhibition. Fourthly, task-switching paradigms have never been connected to depletion research. While the dual-task paradigm examines effects of engaging in one task after the other, participants in task-switching paradigms have to rapidly and repeatedly switch between two (or more) tasks. Fifthly, there is also little integration of research on depletion and mental fatigue. This phenomenon is examined by measuring continuous performance on a single task for up to two hours (Boksem, Meijman, & Lorist, 2006; Hockey & Earle, 2006). It seems that mental fatigue, although very similar to self-control exertion on a conceptual, takes much longer to impair performance. It could be that switching to a new set of task rules propagates performance drops. This would be in sline with our propositions from the second study, namely that sustained connectivity between task-related areas after depletion hinders adjusting to new task demands. This hypothesis could be tested by comparing performance changes in single-task (no task switch), dual-task (one task switch), and task-switching (multiple task switches) paradigms. Performance decrements should appear the fastest for a condition with multiple

task switches, and slowest for a condition with no task switch. Sixthly, the proposed mechanism of depletion effects, namely that sustained connectivity between regulatory and task-specific areas temporarily hampers the capability of regulatory areas to switch their influence to other brain areas and thus to adjust to new task demands, is preliminary and should be examined further. Brain connectivity measurements have so far been mainly employed during states of rest, yet it has been suggested that task-based connectivity is possible and reliable (Smith et al., 2009; Whitfield-Gabrieli & Nieto-Castanon, 2012). Thus our proposition could be tested more directly by examining connectivity during the first and second task in the dual-task paradigm. Seventhly, individual differences have received little attention so far, although differences in trait self-control and a few depletion studies (Job et al., 2010; Salmon, Adriaanse, De Vet, Fennis, & De Ridder, 2014) suggest that differences in depletion susceptibility might play an important role in explaining the effect. Eighthly, depletion effects have so far not been studied in clinical populations, although altered impulse control is a core symptom of some mental disorders. On the one hand, patients with anorexia nervosa demonstrate astounding self-control, with hardly any failure to restrain calorie intake. Critically, they are also successful in periods of hunger, which might share some similarities with states of depletion. Neuroscientific studies have reported increased connectivity among regions implicated in cognitive control and less subcortical reactivity to rewards (Cowdrey, Filippini, Park, Smith, & Mccabe, 2014; Wierenga et al., 2015). Hence one could examine if anorectic patients are less susceptible to depletion effects. On the other hand, patients with addictive disorders might be particularly susceptible to depletion. One of the biggest problems in treatment is the high occurrence of relapses, which might be related to states of self-control depletion. Ninthly and last, a shortcoming of the self-control exertion research is that all findings stem from

laboratory experiments. Self-reports suggest that self-control exertion has negative consequences on subsequent self-control attempts in real-life situations (Hofmann, Vohs, & Baumeister, 2012). Yet there is no study which makes a direct connection between self-control exertion as measured in the lab, and behavior in everyday life.

For example, addressing points seven to nine, an interesting endeavor could be to study depletion effects in smokers who want to quit. Adapting an individual differences approach, one could investigate the predictive power of depletion sensitivity measured in a controlled lab setting for self-control behavior in everyday life. Focusing on smokers would have the advantage that there would be a clear marker of self-control in the real world: the number of smoked cigarettes. For analogous reasons, dieters or drug users would also be ideal clinical study populations. In the first part of the study, self-control and self-control exertion would be measured with the dual-task paradigm. Participants would have to down-regulate their desire to smoke (craving) while pictures of cigarettes and people smoking would be presented, once after a self-control demanding task (self-control exertion condition), and once after a control task (control condition). A within-subject design would be advantageous to be able to control for variability in baseline brain activity and with regard to statistical power in general. With the help of fMRI measurements and a focus on limbic areas related to impulsive behavior (e.g. nucleus accumbens) and lateral prefrontal areas implicated in control, one could quantify participants' success in controlling their craving. Next, similar to Hofman, Vohs, and Baumeister (2012), experience sampling would be used to assess current exertion of self-control, temptations, and consumption (smoked cigarettes) several times daily. With multi-level model analyses similar to Berkman, Falk, and Lieberman (2011), one could examine if the neural data moderates the connection between temptations at one time point and consumption at the

next time point, and if the neural data predict overall consumption. One could also examine whether measuring regulation in a state of self-control exertion can explain more variance in the real-life data than measuring self-control in the control condition. This would be interesting because it would test how meaningful self-control exertion effects are for everyday life.

3.5 Conclusion

Self-control is one of the most important psychological predictors for success in life (Duckworth, 2011). Research suggests that self-control strength fluctuates over time. Specifically, individuals are worse at self-control if they had to control themselves previously (Hagger et al., 2010). The strength model explains these findings by referring to a self-control resource, which becomes depleted with use and replenishes during rest (Baumeister, 2014). This model has been criticized and various alternative models have been proposed, which reject the resource concept in favor of motivational explanations for self-control failure (Inzlicht et al., 2014; Kool & Botvinick, 2014; Kurzban et al., 2013). We conducted three fMRI studies on depletion. In the first study, we manipulated participants' task motivation in addition to their level of self-control exertion. Here we found the usual depletion effect, such that performance was worse after prior self-control exertion. Boosting motivation led participants to overcome the negative consequences of depletion, as has been reported previously. On the neural level, we did not find that motivation canceled out depletion effects, as would be suggested by motivational models of self-control. Instead, motivation and depletion effects had interacting effects on brain activity. This finding is only reconcilable with the assumption of a self-control resource and thus provides support for the strength model. Nevertheless, the physiological basis

of the self-control resource remains unclear. In the second study, we examined effects of self-control exertion on a subsequent resting state. Measuring brain connectivity provided a unique opportunity to study depletion effects in the absence of further task engagement. We found that emotion suppression led to increased connectivity between the IFG and middle temporal gyrus. Both areas are critically involved in emotion regulation. This might reflect sustained connectivity from previous task engagement, suggesting that depletion effects might be related to a temporarily reduced capacity of regulatory areas, such as the IFG, to change their influence to other brain areas. The third study intended to extend effects of self-control exertion on emotional processing to memory formation. It has been reported that depletion increases emotional reactivity in the amygdala (Wagner & Heatherton, 2013). This area is critically involved in encoding of emotional experiences to memory and we thus hypothesized that depletion should enhance emotional memory. Even though our study design was based on the fMRI study which reported increased amygdala reactivity after self-control exertion, we found no evidence for this effect. Consequently, emotional memory was also unaffected by the depletion manipulation. We concluded that increases in amygdala reactivity might not be a reliable consequence of self-control exertion. A review of fMRI studies revealed that depletion effects are mainly found in the IFG and MFG, which are implicated in regulatory processes and attentional control/response selection, respectively. These areas are main hubs within the cognitive control network (Nee et al., 2007) and their high-level functionality supports the assumption of a domain-general self-control resource. However, not all of my study projects were successful at inducing depletion, which is mirrored by an emerging debate about the reliability of depletion effects. Meta-analytic tests suggest that the depletion effect has been overestimated due to a publication bias. Correction techniques arrive at widely different estimations of the magnitude of the depletion effect (Carter et al., 2015;

Inzlicht et al., 2015). Future research should thus focus on replicating published depletion studies and on implementing studies with high statistical power by using big samples and exploring within-subject designs. If replication projects produce significant effect sizes, it would be interesting to see studies which connect depletion to real-life outcomes and which explore ways to assess self-control exertion "outside" of the dual-task paradigm.

4 References

Aharoni, E., Vincent, G. M., Harenski, C. L., Calhoun, V. D., Sinnott-Armstrong, W., Gazzaniga, M. S., & Kiehl, K. A. (2013). Neuroprediction of future rearrest. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 6223–6228. http://doi.org/10.1073/pnas.1219302110

Albert, N. B., Robertson, E. M., & Miall, R. C. (2009). The resting human brain and motor learning. *Current Biology*, *19*, 1023–1027. http://doi.org/10.1016/j.cub.2009.04.028

Amaro, E., & Barker, G. J. (2006). Study design in fMRI: Basic principles. *Brain and Cognition*, *60*, 220–32. http://doi.org/10.1016/j.bandc.2005.11.009

Aron, A. R. (2007). The neural basis of inhibition in cognitive control. *The Neuroscientist*, *13*, 214–228. http://doi.org/10.1177/1073858407299288

Aron, A. R., Behrens, T. E., Smith, S., Frank, M. J., & Poldrack, R. A. (2007). Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. *The Journal of Neuroscience*, *27*, 3743–3752. http://doi.org/10.1523/JNEUROSCI.0519-07.2007

Aron, A. R., Durston, S., Eagle, D. M., Logan, G. D., Stinear, C. M., & Stuphorn, V. (2007). Converging evidence for a fronto-basal-ganglia network for inhibitory control of action and cognition. *Journal of Neuroscience*, *27*, 11860–11864. http://doi.org/10.1523/JNEUROSCI.3644-07.2007

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*, 170–177. http://doi.org/10.1016/j.tics.2004.02.010

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Right inferior frontal cortex: Addressing the rebuttals. *Frontiers in Human Neuroscience*, *8*, 8–11. http://doi.org/10.3389/fnhum.2014.00905

References

Barutchu, A., Carter, O., Hester, R., & Levy, N. (2013). Strength in cognitive self-regulation. *Frontiers in Psychology*, *4*, 174. http://doi.org/10.3389/fpsyg.2013.00174

Baumeister, R. F. (2002). Ego Depletion and Self-Control Failure: An Energy Model of the Self's Executive Function. *Self and Identity*, *1*, 129–136. http://doi.org/10.1080/152988602317319302

Baumeister, R. F. (2014). Self-regulation, ego depletion, and inhibition. *Neuropsychologia*, *65*, 313–319. http://doi.org/10.1016/j.neuropsychologia.2014.08.012

Baumeister, R. F., Bratslavsky, E., Muraven, M., & Tice, D. M. (1998). Ego depletion: Is the active self a limited resource? *Journal of Personality and Social Psychology*, *74*, 1252–1265. http://doi.org/http://dx.doi.org/10.1037//0022-3514.74.5.1252

Baumeister, R. F., & Heatherton, T. F. (1996). Self-regulation failure: An overview. *Psychological Inquiry*, *7*, 1–15. http://doi.org/10.1207/s15327965pli0701_1

Baumeister, R. F., & Vohs, K. D. (2007). Self-regulation, ego depletion, and motivation. *Social and Personality Psychology Compass*, *1*, 115–128. http://doi.org/10.1111/j.1751-9004.2007.00001.x

Baumeister, R. F., Vohs, K. D., & Tice, D. M. (2007). The strength model of self-control. *Current Directions in Psychological Science*, *16*, 351–355. http://doi.org/10.1111/j.1467-8721.2007.00534.x

Beedie, C. J., & Lane, A. M. (2012). The role of glucose in self-control: Another look at the evidence and an alternative conceptualization. *Personality and Social Psychology Review*, *16*, 143–153. http://doi.org/10.1177/1088868311419817

Behzadi, Y., Restom, K., Liau, J., & Liu, T. T. (2007). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*, *37*, 90–101. http://doi.org/10.1016/j.neuroimage.2007.04.042

References

Berkman, E. T., Falk, E. B., & Lieberman, M. D. (2011). In the trenches of real-world self-control: Neural correlates of breaking the link between craving and smoking. *Psychological Science*, *22*, 498–506. http://doi.org/10.1177/0956797611400918

Binder, J., de Quervain, D. J.-F. F., Friese, M., Luechinger, R., Boesiger, P., & Rasch, B. (2012). Emotion suppression reduces hippocampal activity during successful memory encoding. *NeuroImage*, *63*, 525–532. http://doi.org/10.1016/j.neuroimage.2012.07.007

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2006). Mental fatigue, motivation and action monitoring. *Biological Psychology*, *72*, 123–132. http://doi.org/10.1016/j.biopsycho.2005.08.007

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*, 539–546. http://doi.org/10.1016/j.tics.2004.10.003

Botvinick, M. M., Huffstetler, S., & McGuire, J. T. (2009). Effort discounting in human nucleus accumbens. *Cognitive, Affective, & Behavioral Neuroscience*, *9*, 16–27. http://doi.org/10.3758/CABN.9.1.16

Botvinick, M. M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection- for-action in anterior cingulate cortex. *Nature*, *402*, 179–181. http://doi.org/http://dx.doi.org/10.1038/46035

Bray, S. R., Martin Ginis, K. a, Hicks, A. L., & Woodgate, J. (2008). Effects of self-regulatory strength depletion on muscular performance and EMG activation. *Psychophysiology*, *45*, 337–343. http://doi.org/10.1111/j.1469-8986.2007.00625.x

Brzezicka, A., Kaminski, J., & Wróbelb, A. (2013). Local resource depletion hypothesis as a mechanism for action selection in the brain. *Behavioral and Brain Sciences*, *36*, 682–683. http://doi.org/http://dx.doi.org/10.1017/s0140525x13000940

Buhle, J. T., Silvers, J. A., Wager, T. D., Lopez, R., Onyemekwu, C., Kober, H., … Ochsner, K. N. (2014). Cognitive reappraisal of emotion: A meta-analysis of human

neuroimaging studies. *Cerebral Cortex*, *24*, 1–10. http://doi.org/10.1093/cercor/bht154

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*, 1394–1402. http://doi.org/10.1006/nimg.2002.1280

Cahill, L., Babinsky, R., Markowitsch, H. J., & McGaugh, J. L. (1995). The amygdala and emotional memory. *Nature*, *377*, 295–296. http://doi.org/http://dx.doi.org/10.1038/377295a0

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D. E., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *The Journal of Neuroscience*, *20*, RC99 (1–5). Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11000199

Carter, E. C., Kofler, L. M., Forster, D. E., & McCullough, M. E. (2015). A series of meta-analytic tests of the depletion effect: Self-control does not seem to rely on a limited resource. *Journal of Experimental Psychology: General*, *144*, 796–815. http://doi.org/10.1037/xge0000083

Carter, E. C., & McCullough, M. E. (2013). Is ego depletion too incredible? Evidence for the overestimation of the depletion effect. *Behavioral and Brain Sciences*, *36*, 683–684. http://doi.org/http://dx.doi.org/10.1017/s0140525x13000952

Carter, E. C., & McCullough, M. E. (2014). Publication bias and the limited strength model of self-control: Has the evidence for ego depletion been overestimated? *Frontiers in Psychology*, *5*, 1–11. http://doi.org/10.3389/fpsyg.2014.00823

Cauda, F., Cavanna, A. E., D'agata, F., Sacco, K., Duca, S., & Geminiani, G. C. (2011). Functional connectivity and coactivation of the nucleus accumbens: A combined functional connectivity and structure-based meta-analysis. *Journal of Cognitive Neuroscience*, *23*, 2864–2877. http://doi.org/10.1162/jocn.2011.21624

References

Chai, X. J., Castañán, A. N., Öngür, D., & Whitfield-Gabrieli, S. (2012). Anticorrelations in resting state networks without global signal regression. *NeuroImage*, *59*, 1420–1428. http://doi.org/10.1016/j.neuroimage.2011.08.048

Clithero, J. A., Reeck, C., Carter, R. M., Smith, D. V, & Huettel, S. A. (2011). Nucleus accumbens mediates relative motivation for rewards in the absence of choice. *Frontiers in Human Neuroscience*, *5*, 87. http://doi.org/10.3389/fnhum.2011.00087

Cohen, D. B., & Saling, L. L. (2013). Maximising utility does not promote survival. *Behavioral and Brain Sciences*, *36*, 685. http://doi.org/http://dx.doi.org/10.1017/s0140525x13000976

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Lawrence Erlbaum Associates.

Cowdrey, F. a., Filippini, N., Park, R. J., Smith, S. M., & Mccabe, C. (2014). Increased resting state functional connectivity in the default mode network in recovered anorexia nervosa. *Human Brain Mapping*, *35*, 483–491. http://doi.org/10.1002/hbm.22202

Cox, S. R., Bastin, M. E., Ferguson, K. J., Allerhand, M., Royle, N. a, Maniega, S. M., … MacPherson, S. E. (2014). Compensation or inhibitory failure? Testing hypotheses of age-related right frontal lobe involvement in verbal memory ability using structural and diffusion MRI. *Cortex*, *63C*, 4–15. http://doi.org/10.1016/j.cortex.2014.08.001

Craig, A. D. B. (2009). How do you feel-now? The anterior insula and human awareness. *Nature Reviews. Neuroscience*, *10*, 59–70. http://doi.org/10.1038/nrn2555

De Luca, M., Beckmann, C. F., De Stefano, N., Matthews, P. M., & Smith, S. M. (2006). fMRI resting state networks define distinct modes of long-distance interactions in the human brain. *NeuroImage*, *29*, 1359–1567. http://doi.org/10.1016/j.neuroimage.2005.08.035

De Simoni, C., Luethi, M. S., & Von Bastian, C. (in preparation). No evidence for depletion effects in a wide range cognitive tasks.

References

De Zubicaray, G. I., Andrew, C., Zelaya, F. O., Williams, S. C. R., & Dumanoir, C. (2000). Motor response suppression and the prepotent tendency to respond: A parametric fMRI study. *Neuropsychologia*, *38*, 1280–1291. http://doi.org/10.1016/S0028-3932(00)00033-6

Delgado, M. R., Nearing, K. I., LeDoux, J. E., & Phelps, E. A. (2008). Neural circuitry underlying the regulation of conditioned fear and its relation to extinction. *Neuron*, *59*, 829–838. http://doi.org/10.1016/j.neuron.2008.06.029

Demos, K. E., Heatherton, T. F., & Kelley, W. M. (2012). Individual differences in nucleus accumbens activity to food and sexual images predict weight gain and sexual behavior. *Journal of Neuroscience*, *32*, 5549–5552. http://doi.org/10.1523/JNEUROSCI.5958-11.2012

Derrfuss, J., Brass, M., Neumann, J., & von Cramon, D. Y. (2005). Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies. *Human Brain Mapping*, *25*, 22–34. http://doi.org/10.1002/hbm.20127

DeWall, C. N., Baumeister, R. F., Stillman, T. F., & Gailliot, M. T. (2007). Violence restrained: Effects of self-regulation and its depletion on aggression. *Journal of Experimental Social Psychology*, *43*, 62–76. http://doi.org/10.1016/j.jesp.2005.12.005

Diekhof, E. K., Geier, K., Falkai, P., & Gruber, O. (2011). Fear is only as deep as the mind allows. A coordinate-based meta-analysis of neuroimaging studies on the regulation of negative affect. *NeuroImage*, *58*, 275–285. http://doi.org/10.1016/j.neuroimage.2011.05.073

Duckworth, A. L. (2011). The significance of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 2639–2640. http://doi.org/10.1073/pnas.1019725108

Durston, S., Thomas, K. M., Worden, M. S., Yang, Y., & Casey, B. J. (2002). The effect of preceding context on inhibition: An event-related fMRI study. *NeuroImage*, *16*, 449–453. http://doi.org/10.1006/nimg.2002.1074

Duval, S., & Tweedie, R. (2000). Trim and fill: A simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. *Biometrics*, *56*, 455–63. http://doi.org/http://dx.doi.org/10.1111/j.0006-341x.2000.00455.x

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ*, *315*, 629–634. http://doi.org/10.1136/bmj.315.7109.629

Ersche, K. D., Williams, G. B., Robbins, T. W., & Bullmore, E. T. (2013). Meta-analysis of structural brain abnormalities associated with stimulant drug dependence and neuroimaging of addiction vulnerability and resilience. *Current Opinion in Neurobiology*, *23*, 615–624. http://doi.org/10.1016/j.conb.2013.02.017

Esposito, F., Otto, T., Zijlstra, F. R. H., & Goebel, R. (2014). Spatially distributed effects of mental exhaustion on resting-state fMRI networks. *PloS One*, *9*, e94222. http://doi.org/10.1371/journal.pone.0094222

Evers, E. A. T., Klaassen, E. B., Rombouts, S. A., Backes, W. H., & Jolles, J. (2012). The effects of sustained cognitive task performance on subsequent resting state functional connectivity in healthy young and middle-aged male schoolteachers. *Brain Connectivity*, *2*, 102–112. http://doi.org/10.1089/brain.2011.0060

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*, 175–191. http://doi.org/http://dx.doi.org/10.3758/bf03193146

Ferguson, C. J., & Brannick, M. T. (2012). Publication bias in psychological science: Prevalence, methods for identifying and controlling, and implications for the use of meta-analyses. *Psychological Methods*, *17*, 120–128. http://doi.org/10.1037/a0024445

Fischer, P., Greitemeyer, T., & Frey, D. (2008). Self-regulation and selective exposure: The impact of depleted self-regulation resources on confirmatory information

processing. *Journal of Personality and Social Psychology*, *94*, 382–395. http://doi.org/10.1037/0022-3514.94.3.382

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 9673–9678. http://doi.org/10.1073/pnas.0504136102

Fox, P. T., Raichle, M. E., Mintun, M. A., & Dence, C. (1988). Nonoxidative glucose consumption during focal physiologic neural activity. *Science*, *241*, 462–464. http://doi.org/10.1126/science.3260686

Frank, D. W., Dewitt, M., Hudgens-Haney, M., Schaeffer, D. J., Ball, B. H., Schwarz, N. F., … Sabatinelli, D. (2014). Emotion regulation: Quantitative meta-analysis of functional activation and deactivation. *Neuroscience and Biobehavioral Reviews*, *45*, 202–211. http://doi.org/10.1016/j.neubiorev.2014.06.010

Freeman, N., & Muraven, M. (2010). Self-control depletion leads to increased risk taking. *Social Psychological and Personality Science*. http://doi.org/10.1177/1948550609360421

Friese, M., Binder, J., Luechinger, R., Boesiger, P., & Rasch, B. (2013). Suppressing emotions impairs subsequent Stroop performance and reduces prefrontal brain activation. *PLOS ONE*, *8*, e60385. http://doi.org/10.1371/journal.pone.0060385

Friese, M., Hofmann, W., & Wänke, M. (2008). When impulses take over: Moderated predictive validity of explicit and implicit attitude measures in predicting food choice and consumption behaviour. *The British Journal of Social Psychology*, *47*, 397–419. http://doi.org/10.1348/014466607X241540

Friese, M., Messner, C., & Schaffner, Y. (2012). Mindfulness meditation counteracts self-control depletion. *Consciousness and Cognition*, *21*, 1016–1022. http://doi.org/10.1016/j.concog.2012.01.008

References

Friese, M., Schweizer, L., Arnoux, A., Sutter, F., & Wänke, M. (2014). Personal prayer counteracts self-control depletion. *Consciousness and Cognition*, *29*, 90–95. http://doi.org/10.1016/j.jesp.2013.11.006

Fukunaga, M., Horovitz, S. G., Van Gelderen, P., De Zwart, J. A., Jansma, J. M., Ikonomidou, V. N., … Duyn, J. H. (2006). Large-amplitude, spatially correlated fluctuations in BOLD fMRI signals during extended rest and early sleep stages. *Magnetic Resonance Imaging*, *24*, 979–992. http://doi.org/10.1016/j.mri.2006.04.018

Funder, D. C., Levine, J. M., Mackie, D. M., Morf, C. C., Vazire, S., & West, S. G. (2014). Improving the dependability of research in personality and social psychology: Recommendations for research and educational practice. *Personality and Social Psychology Review*, *18*, 3–12. http://doi.org/10.1177/1088868313507536

Gailliot, M. T., & Baumeister, R. F. (2007a). Self-regulation and sexual restraint: Dispositionally and temporarily poor self-regulatory abilities contribute to failures at restraining sexual behavior. *Personality and Social Psychology Bulletin*, *33*, 173–186. http://doi.org/10.1177/0146167206293472

Gailliot, M. T., & Baumeister, R. F. (2007b). The physiology of willpower: Linking blood glucose to self-control. *Personality and Social Psychology Review*, *11*, 303–327. http://doi.org/10.1177/1088868307303030

Gailliot, M. T., Baumeister, R. F., DeWall, C. N., Maner, J. K., Plant, E. A., Tice, D. M., … Schmeichel, B. J. (2007). Self-control relies on glucose as a limited energy source: Willpower is more than a metaphor. *Journal of Personality and Social Psychology*, *92*, 325–336. http://doi.org/10.1037/0022-3514.92.2.325

Garavan, H., Ross, T. J., Murphy, K., Roche, R. a P., & Stein, E. a. (2002). Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. *NeuroImage*, *17*, 1820–1829. http://doi.org/10.1006/nimg.2002.1326

Gehring, W. J., Goss, B., & Coles, M. G. H. (1993). A neural system for error detection and compensation. *Psychological Science*. http://doi.org/10.1111/j.1467-9280.1993.tb00586.x

Gendolla, G. H. E., & Richter, M. (2013). Opportunity costs calculations only determine justified effort - Or, what happened to the resource conservation principle? *Behavioral and Brain Sciences*, *36*, 686–687. http://doi.org/http://dx.doi.org/10.1017/s0140525x13000988

Gervais, W. (2015, June 25). *Putting PET-PEESE to the test [Blog post]*. Retrieved from http://willgervais.com/blog/2015/6/25/putting-pet-peese-to-the-test-1

Ghashghaei, H. T., Hilgetag, C. C., & Barbas, H. (2007). Sequence of information processing for emotions based on the anatomic dialogue between prefrontal cortex and amygdala. *NeuroImage*, *34*, 905–923. http://doi.org/10.1016/j.neuroimage.2006.09.046

Gross, J. J. (2002). Emotion regulation: Affective, cognitive, and social consequences. *Psychophysiology*, *39*, 281–291. http://doi.org/10.1017.S0048577201393198

Gross, J. J., & Thompson, R. A. (2007). Emotion regulation: Conceptual foundations. In J. J. Gross (Ed.), *Handbook of emotion regulation* (pp. 3–24). New York, NY: Guilford Press.

Hagger, M. S., & Chatzisarantis, N. L. D. (2014). It is premature to regard the ego-depletion effect as "Too Incredible." *Frontiers in Psychology*, *5*, 298. http://doi.org/10.1037/a0019486

Hagger, M. S., Wood, C., Stiff, C., & Chatzisarantis, N. L. D. (2010). Ego depletion and the strength model of self-control: A meta-analysis. *Psychological Bulletin*, *136*, 495–525. http://doi.org/10.1037/a0019486

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *NeuroImage*, *50*, 1313–1319. http://doi.org/10.1016/j.neuroimage.2009.12.109

Hare, T. A., Camerer, C. F., & Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. *Science*, *324*, 646–648. http://doi.org/10.1126/science.1168450

Heatherton, T. F., & Wagner, D. D. (2011). Cognitive neuroscience of self-regulation failure. *Trends in Cognitive Sciences*, *15*, 132–139. http://doi.org/10.1016/j.tics.2010.12.005

Hedgcock, W. M., Vohs, K. D., & Rao, A. R. (2012). Reducing self-control depletion effects through enhanced sensitivity to implementation: Evidence from fMRI and behavioral studies. *Journal of Consumer Psychology*, *22*, 486–495. http://doi.org/10.1016/j.jcps.2012.05.008

Hockey, G. R. J., & Earle, F. (2006). Control over the scheduling of simulated office work reduces the impact of workload on mental fatigue and task performance. *Journal of Experimental Psychology: Applied*, *12*, 50–65.

Hofmann, W., Vohs, K. D., & Baumeister, R. F. (2012). What People Desire, Feel Conflicted About, and Try to Resist in Everyday Life. *Psychological Science*, *23*, 582–588. http://doi.org/10.1177/0956797612437426

Inzlicht, M., Gervais, W., & Berkman, E. (2015, September 11). *News of ego depletion's demise is premature: Commentary on Carter, Kofler, Forster, & Mccullough, 2015*. Retrieved from http://ssrn.com/abstract=2659409

Inzlicht, M., & Gutsell, J. N. (2007). Running on empty: Neural signals for self-control failure. *Psychological Science*, *18*, 933–937. http://doi.org/10.1111/j.1467-9280.2007.02004.x

Inzlicht, M., & Schmeichel, B. J. (2012). What is ego depletion? Toward a mechanistic revision of the resource model of self-control. *Perspectives on Psychological Science*, *7*, 450–463. http://doi.org/10.1177/1745691612454134

Inzlicht, M., Schmeichel, B. J., & Macrae, C. N. (2014). Why self-control seems (but may not be) limited. *Trends in Cognitive Sciences*, *18*, 127–133. http://doi.org/10.1016/j.tics.2013.12.009

Ioannidis, J. P. A. (2008). Interpretation of tests of heterogeneity and bias in meta-analysis. *Journal of Evaluation in Clinical Practice*, *14*, 951–7. http://doi.org/10.1111/j.1365-2753.2008.00986.x

Ioannidis, J. P. a. (2012). Why science is not necessarily self-correcting. *Perspectives on Psychological Science*, *7*, 645–654. http://doi.org/10.1177/1745691612464056

Job, V., Bernecker, K., Miketta, S., Friese, M., Job, V., & Bernecker, K. (in press). Implicit theories about willpower predict the activation of a rest goal following self-control exertion. *Journal of Personality and Social Psychology*. http://doi.org/http://dx.doi.org/10.1037/pspp0000042

Job, V., Dweck, C. S., & Walton, G. M. (2010). Ego depletion-is it all in your head? Implicit theories about willpower affect self-regulation. *Psychological Science*, *21*, 1686–1693. http://doi.org/10.1177/0956797610384745

John, L. K., Loewenstein, G., & Prelec, D. (2012). Measuring the prevalence of questionable research practices with incentives for truth telling. *Psychological Science*, *23*, 524–532. http://doi.org/10.1177/0956797611430953

Johnstone, T., van Reekum, C. M., Urry, H. L., Kalin, N. H., & Davidson, R. J. (2007). Failure to regulate: Counterproductive recruitment of top-down prefrontal-subcortical circuitry in major depression. *The Journal of Neuroscience*, *27*, 8877–8884. http://doi.org/10.1523/JNEUROSCI.2063-07.2007

Kensinger, E. a, & Corkin, S. (2004). Two routes to emotional memory: Distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 3310–5. http://doi.org/10.1073/pnas.0306408101

Kerns, J. G., Cohen, J. D., MacDonald, A. W., Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*, 1023–1026. http://doi.org/10.1126/science.1089910

Kidd, C., Palmeri, H., & Aslin, R. N. (2013). Rational snacking: Young children's decision-making on the marshmallow task is moderated by beliefs about environmental

reliability. *Cognition*, *126*, 109–114. http://doi.org/10.1016/j.cognition.2012.08.004

Kober, H., Mende-siedlecki, P., Kross, E. F., Weber, J., Mischel, W., Hart, C. L., & Ochsner, K. N. (2010). Prefrontal-striatal pathway underlies cognitive regulation of craving. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 14811–14816. http://doi.org/10.1073/pnas.1007779107

Kohn, N., Eickhoff, S. B., Scheller, M., Laird, a. R., Fox, P. T., & Habel, U. (2014). Neural network of cognitive emotion regulation - An ALE meta-analysis and MACM analysis. *NeuroImage*, *87*, 345–355. http://doi.org/10.1016/j.neuroimage.2013.11.001

Kool, W., & Botvinick, M. M. (2013). The intrinsic cost of cognitive control. *Behavioral and Brain Sciences*, *36*, 697–698. http://doi.org/10.1017/S0140525X1300109X

Kool, W., & Botvinick, M. M. (2014). A labor/leisure tradeoff in cognitive control. *Journal of Experimental Psychology: General*, *143*, 131–141. http://doi.org/10.1037/a0031048

Kurzban, R. (2010). Does the brain consume additional glucose during self-control tasks? *Evolutionary Psychology*, *8*, 244–259.

Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences*, *36*, 661–679. http://doi.org/10.1017/S0140525X12003196

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews. Neuroscience*, *7*, 54–64. http://doi.org/10.1038/nrn1825

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8*. *University of Florida, Gainesville, FL*.

LeDoux, J. (2007). The amygdala. *Current Biology*, *17*, 868–874. http://doi.org/10.1016/j.cub.2007.08.005

Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, *35*, 1219–1236. http://doi.org/10.1016/j.neubiorev.2010.12.012

Luethi, M. S., Friese, M., Binder, J., Boesiger, P., Luechinger, R., & Rasch, B. (submitted). Motivational incentives lead to an over-increase in lateral prefrontal activity after self-control exertion.

Luethi, M. S., Friese, M., Schroeder, C., Ribaut, N., Boesiger, P., Luechinger, R., & Rasch, B. (submitted). No effect of self-control exertion on amygdala reactivity and emotional memory.

Maldjian, J. A., Laurienti, P. J., & Burdette, J. H. (2004). Precentral gyrus discrepancy in electronic versions of the Talairach atlas. *NeuroImage*, *21*, 450–455. http://doi.org/10.1016/j.neuroimage.2003.09.032

Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, *315*, 393–395. http://doi.org/10.1126/science.1131295

Matsumoto, D., Yoo, S. H., & Nakagawa, S. (2008). Culture, emotion regulation, and adjustment. *Journal of Personality and Social Psychology*, *94*, 925–937. http://doi.org/10.1037/0022-3514.94.6.925

McGaugh, J. L. (2000). Memory-A century of consolidation. *Science*, *287*, 248–251. http://doi.org/10.1126/science.287.5451.248

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, *27*, 1–28. http://doi.org/10.1146/annurev.neuro.27.070203.144157

McGuire, J. T., & Botvinick, M. M. (2010). Prefrontal cortex, cognitive control, and the registration of decision costs. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 7922–7926. http://doi.org/10.1073/pnas.0910662107

McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *NeuroImage*, *61*, 1277–1286. http://doi.org/10.1016/j.neuroimage.2012.03.068

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202. http://doi.org/10.1146/annurev.neuro.24.1.167

Mischel, W., Shoda, Y., & Rodriguez, M. L. (1989). Delay of gratification in children. *Science*, *244*, 933–938. http://doi.org/http://dx.doi.org/10.1126/science.2658056

Mitchell, J. P., Heatherton, T. F., Kelley, W. M., Wyland, C. L., Wegner, D. M., & Neil Macrae, C. (2007). Separating sustained from transient aspects of cognitive control during thought suppression. *Psychological Science*, *18*, 292–297. http://doi.org/10.1111/j.1467-9280.2007.01891.x

Moffitt, T. E., Arseneault, L., Belsky, D., Dickson, N., Hancox, R. J., Harrington, H., … Caspi, A. (2011). A gradient of childhood self-control predicts health, wealth, and public safety. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 2693–2698. http://doi.org/10.1073/pnas.1010076108

Molden, D. C., Hui, C. M., Scholer, A. A., Meier, B. P., Noreen, E. E., D'Agostino, P. R., & Martin, V. (2012). Motivational versus metabolic effects of carbohydrates on self-control. *Psychological Science*, *23*, 1137–1144. http://doi.org/10.1177/0956797612439069

Moreno, S. G., Sutton, A. J., Ades, A. E., Stanley, T. D., Abrams, K. R., Peters, J. L., & Cooper, N. J. (2009). Assessment of regression-based methods to adjust for publication bias through a comprehensive simulation study. *BMC Medical Research Methodology*, *9*, 2. http://doi.org/10.1186/1471-2288-9-2

Mullette-Gillman, O. a, Detwiler, J. M., Winecoff, A., Dobbins, I., & Huettel, S. a. (2011). Infrequent, task-irrelevant monetary gains and losses engage dorsolateral and

ventrolateral prefrontal cortex. *Brain Research*, *1395*, 53–61. http://doi.org/10.1016/j.brainres.2011.04.026

Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: Does self-control resemble a muscle? *Psychological Bulletin*, *126*, 247–259. http://doi.org/10.1037/0033-2909.126.2.247

Muraven, M., Shmueli, D., & Burkley, E. (2006). Conserving self-control strength. *Journal of Personality and Social Psychology*, *91*, 524–537. http://doi.org/10.1037/0022-3514.91.3.524

Muraven, M., & Slessareva, E. (2003). Mechanisms of self-control failure: Motivation and limited resources. *Personality and Social Psychology Bulletin*, *29*, 894–906. http://doi.org/10.1177/0146167203253209

Muraven, M., Tice, D. M., & Baumeister, R. F. (1998). Self-control as limited resource: Regulatory depletion patterns. *Journal of Personality and Social Psychology*, *74*, 774–789. http://doi.org/10.1037/0022-3514.74.3.774

Muschelli, J., Nebel, M. B., Caffo, B. S., Barber, A. D., Pekar, J. J., & Mostofsky, S. H. (2014). Reduction of motion-related artifacts in resting state fMRI using aCompCor. *NeuroImage*, *96*, 22–35. http://doi.org/10.1016/j.neuroimage.2014.03.028

Myrseth, K. O. R., & Fishbach, A. (2009). Self-control: A function of knowing when and how to excercise restraint. *Current Directions in Psychological Science*, *18*, 247–252. http://doi.org/10.1111/j.1467-8721.2009.01645.x

Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*, 1–17. http://doi.org/10.3758/CABN.7.1.1

Ochsner, K. N., Silvers, J. A., & Buhle, J. T. (2012). Functional imaging studies of emotion regulation: A synthetic review and evolving model of the cognitive control of emotion. *Annals of the New York Academy of Sciences*, *1251*, E1–E24. http://doi.org/10.1111/j.1749-6632.2012.06751.x

Persson, J., Larsson, A., & Reuter-Lorenz, P. A. (2013). Imaging fatigue of interference control reveals the neural basis of executive resource depletion. *Journal of Cognitive Neuroscience*, *25*, 338–351. http://doi.org/10.1162/jocn_a_00321

Persson, J., Welsh, K. M., Jonides, J., & Reuter-Lorenz, P. A. (2007). Cognitive fatigue of executive processes: Interaction between interference resolution tasks. *Neuropsychologia*, *45*, 1571–1579. http://doi.org/10.1055/s-0029-1237430.Imprinting

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage*, *16*, 331–348. http://doi.org/10.1006/nimg.2002.1087

Phelps, E. a. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annual Review of Psychology*, *57*, 27–53. http://doi.org/10.1146/annurev.psych.56.091103.070234

Prvulovic, D., Van de Ven, V., Sack, A. T., Maurer, K., & Linden, D. E. J. (2005). Functional activation imaging in aging and dementia. *Psychiatry Research*, *140*, 97–113. http://doi.org/10.1016/j.pscychresns.2005.06.006

Pyka, M., Beckmann, C. F., Schöning, S., Hauke, S., Heider, D., Kugel, H., … Konrad, C. (2009). Impact of working memory load on fMRI resting state pattern in subsequent resting phases. *PLoS ONE*, *4*. http://doi.org/10.1371/journal.pone.0007198

Raichle, M. E., & Mintun, M. A. (2006). Brain work and brain imaging. *Annual Review of Neuroscience*, *29*, 449–476. http://doi.org/10.1146/annurev.neuro.29.051605.112819

Raichle, M. E., & Snyder, A. Z. (2007). A default mode of brain function: A brief history of an evolving idea. *NeuroImage*, *37*, 1083–1090. http://doi.org/10.1016/j.neuroimage.2007.02.041

Rasch, B., Spalek, K., Buholzer, S., Luechinger, R., Boesiger, P., & Papassotiropoulos, A. (2009). A genetic variation of the noradrenergic system is related to differential amygdala activation, *106*, 19191–19196.

Richards, J. M. (2004). The cognitive consequences of concealing feelings. *Psychological Science*, *13*, 131–134. http://doi.org/10.1111/j.0963-7214.2004.00291.x

Richards, J. M., & Gross, J. J. (2006). Personality and emotional memory: How regulating emotion impairs memory for emotional events. *Journal of Research in Personality*, *40*, 631–651. http://doi.org/10.1016/j.jrp.2005.07.002

Rosenberg, M. S. (2005). The file-drawer problem revisited: A general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, *59*, 464–468. http://doi.org/http://dx.doi.org/10.1554/04-602

Rossion, B., Schiltz, C., & Crommelinck, M. (2003). The functionally defined right occipital and fusiform "face areas" discriminate novel from visually familiar faces. *NeuroImage*, *19*, 877–883. http://doi.org/10.1016/S1053-8119(03)00105-8

Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., … Taylor, E. (2001). Mapping motor inhibition: Conjunctive brain activations across different versions of go/no-go and stop tasks. *NeuroImage*, *13*, 250–261. http://doi.org/10.1006/nimg.2000.0685

Rubia, K., Smith, A. B., Brammer, M. J., & Taylor, E. (2003). Right inferior prefrontal cortex mediates response inhibition while mesial prefrontal cortex is responsible for error detection. *NeuroImage*, *20*, 351–358. http://doi.org/10.1016/S1053-8119(03)00275-1

Rücker, G., Carpenter, J. R., & Schwarzer, G. (2011). Detecting and adjusting for small-study effects in meta-analysis. *Biometrical Journal. Biometrische Zeitschrift*, *53*, 351–68. http://doi.org/10.1002/bimj.201000151

Salmon, S. J., Adriaanse, M. a, De Vet, E., Fennis, B. M., & De Ridder, D. T. D. (2014). "When the going gets tough, who keeps going?" Depletion sensitivity moderates the ego-

depletion effect. *Frontiers in Psychology*, *5*, 647. http://doi.org/10.3389/fpsyg.2014.00647

Sämann, P. G., Wehrle, R., Hoehn, D., Spoormaker, V. I., Peters, H., Tully, C., … Czisch, M. (2011). Development of the brain's default mode network from wakefulness to slow wave sleep. *Cerebral Cortex*, *21*, 2082–2093. http://doi.org/10.1093/cercor/bhq295

Sanders, M. A., Shirk, S. D., Burgin, C. J., & Martin, L. L. (2012). The gargle effect: Rinsing the mouth with glucose enhances self-control. *Psychological Science*, *23*, 1470–1472. http://doi.org/10.1177/0956797612450034

Schlam, T. R., Wilson, N. L., Shoda, Y., Mischel, W., & Ayduk, O. (2013). Preschoolers' delay of gratification predicts their body mass 30 years later. *Journal of Pediatrics*, *162*, 90–93. http://doi.org/10.1016/j.jpeds.2012.06.049

Schmeichel, B. J. (2007). Attention control, memory updating, and emotion regulation temporarily reduce the capacity for executive control. *Journal of Experimental Psychology: General*, *136*, 241–255. http://doi.org/10.1037/0096-3445.136.2.241

Schmeichel, B. J., & Vohs, K. D. (2009). Self-affirmation and self-control: Affirming core values counteracts ego depletion. *Journal of Personality and Social Psychology*, *96*, 770–782. http://doi.org/10.1037/a0014635

Schmeichel, B. J., Vohs, K. D., & Baumeister, R. F. (2003). Intellectual performance and ego depletion: Role of the self in logical reasoning and other information processing. *Journal of Personality and Social Psychology*, *85*, 33–46. http://doi.org/10.1037/0022-3514.85.1.33

Schoenbaum, G., Takahashi, Y., Liu, T. L., & Mcdannald, M. a. (2011). Does the orbitofrontal cortex signal value? *Annals of the New York Academy of Sciences*, *1239*, 87–99. http://doi.org/10.1111/j.1749-6632.2011.06210.x

Schroeder, S. A. (2007). We can do better - Improving the health of the American people. *New England Journal of Medicine*, *357*, 1221–1228. http://doi.org/10.1056/nejmsa073350

Shmueli, D., & Prochaska, J. J. (2009). Resisting tempting foods and smoking behavior: Implications from a self-control theory perspective. *Health Psychology*, *28*, 300–306. http://doi.org/10.1037/a0013826

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology: undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science*, *22*, 1359–1366. http://doi.org/10.1177/0956797611417632

Simons, D. J. (2014). The value of direct replication. *Perspectives on Psychological Science*, *9*, 76–80. http://doi.org/10.1177/1745691613514755

Simonsohn, U., Nelson, L. D., & Simmons, J. P. (2014). p-Curve and effect size: Correcting for publication bias using only significant results. *Perspectives on Psychological Science*, *9*, 666–681. http://doi.org/10.1177/1745691614553988

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., … Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 13040–13045. http://doi.org/10.1073/pnas.0905267106

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*, 195–231.

Stanley, T. D., Jarrell, S. B., & Doucouliagos, H. (2010). Could it be better to discard 90% of the data? A statistical paradox. *The American Statistician*, *64*, 70–77. http://doi.org/10.1198/tast.2009.08205

Stevens, W. D., Buckner, R. L., & Schacter, D. L. (2010). Correlated low-frequency BOLD fluctuations in the resting human brain are modulated by recent experience in category-preferential visual regions. *Cerebral Cortex*, *20*, 1997–2006. http://doi.org/10.1093/cercor/bhp270

Swann, N., Tandon, N., Canolty, R., Ellmore, T. M., McEvoy, L. K., Dreyer, S., … Aron, A. R. (2009). Intracranial EEG reveals a time- and frequency-specific role for the right inferior frontal gyrus and primary motor cortex in stopping initiated responses. *The*

Journal of Neuroscience, *29*, 12675–12685. http://doi.org/10.1523/JNEUROSCI.3359-09.2009

Swick, D., Ashley, V., & Turken, A. U. (2008). Left inferior frontal gyrus is critical for response inhibition. *BMC Neuroscience*, *9*, 102. http://doi.org/10.1186/1471-2202-9-102

Swick, D., Ashley, V., & Turken, U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *NeuroImage*, *56*, 1655–1665. http://doi.org/10.1016/j.neuroimage.2011.02.070

Swick, D., & Chatham, C. H. (2014). Ten years of inhibition revisited. *Frontiers in Human Neuroscience*, *8*, 115–116. http://doi.org/10.1038/nn1003

Tabibnia, G., Creswell, J. D., Kraynak, T. E., Westbrook, C., Julson, E., & Tindle, H. A. (2014). Common prefrontal regions activate during self-control of craving, emotion, and motor impulses in smokers. *Clinical Psychological Science*, *2*, 611–619. http://doi.org/10.1177/2167702614522037

Tabibnia, G., Monterosso, J. R., Baicy, K., Aron, A. R., Poldrack, R. A., Chakrapani, S., … London, E. D. (2011). Different forms of self-control share a neurocognitive substrate. *Journal of Neuroscience*, *31*, 4805–4810. http://doi.org/10.1523/JNEUROSCI.2859-10.2011

Tambini, A., Ketz, N., & Davachi, L. (2010). Enhanced brain correlations during rest are related to memory for recent experiences. *Neuron*, *65*, 280–290. http://doi.org/10.1016/j.neuron.2010.01.001

Tice, D. M., Baumeister, R. F., Shmueli, D., & Muraven, M. (2007). Restoring the self: Positive affect helps improve self-regulation following ego depletion. *Journal of Experimental Social Psychology*, *43*, 379–384. http://doi.org/10.1016/j.jesp.2006.05.007

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., … Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a

macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*, 273–289. http://doi.org/10.1006/nimg.2001.0978

Ullsperger, M., Harsay, H. a., Wessel, J. R., & Ridderinkhof, K. R. (2010). Conscious perception of errors and its relation to the anterior insula. *Brain Structure and Function*, 1–15. http://doi.org/10.1007/s00429-010-0261-1

Urry, H. L., van Reekum, C. M., Johnstone, T., Kalin, N. H., Thurow, M. E., Schaefer, H. S., … Davidson, R. J. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *The Journal of Neuroscience*, *26*, 4415–4425. http://doi.org/10.1523/JNEUROSCI.3215-05.2006

Van Der Laan, L. N., De Ridder, D. T. D., Viergever, M. A., & Smeets, P. A. M. (2011). The first taste is always with the eyes: A meta-analysis on the neural correlates of processing visual food cues. *NeuroImage*, *55*, 296–303. http://doi.org/10.1016/j.neuroimage.2010.11.055

Van Veen, V., & Carter, C. S. (2002). The anterior cingulate as a conflict monitor: FMRI and ERP studies. *Physiology and Behavior*, *77*, 477–482. http://doi.org/10.1016/S0031-9384(02)00930-7

Van Veen, V., & Miller, E. K. (2007). Anterior cingulate cortex and conflict detection : An update of theory and data, *7*, 367–379. http://doi.org/http://dx.doi.org/10.3758/cabn.7.4.367

Vohs, K. D., Baumeister, R. F., & Ciarocco, N. J. (2005). Self-regulation and self-presentation: Regulatory resource depletion impairs impression management and effortful self-presentation depletes regulatory resources. *Journal of Personality and Social Psychology*, *88*, 632–57. http://doi.org/10.1037/0022-3514.88.4.632

Vohs, K. D., Baumeister, R. F., & Schmeichel, B. J. (2013). Erratum to “Motivation, personal beliefs, and limited resources all contribute to self-control.” *Journal of Experimental Social Psychology*, *49*, 184–188. http://doi.org/10.1016/j.jesp.2012.08.007

Vohs, K. D., & Heatherton, T. F. (2000). Self-regulatory failure: A resource-depletion approach. *Psychological Science*, *11*, 249–254. http://doi.org/10.1111/1467-9280.00250

Volkow, N. D., & Baler, R. D. (2012). To stop or not to stop? *Science*, *335*, 546–548. http://doi.org/10.1126/science.1218170

Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia*, *45*, 174–194. http://doi.org/10.1016/j.neuropsychologia.2006.06.003

Wagner, D. D., Altman, M., Boswell, R. G., Kelley, W. M., & Heatherton, T. F. (2013). Self-regulatory depletion enhances neural responses to rewards and impairs top-down control. *Psychological Science*, *24*, 2262–2271. http://doi.org/10.1177/0956797613492985

Wagner, D. D., & Heatherton, T. F. (2013). Self-regulatory depletion increases emotional reactivity in the amygdala. *Social Cognitive And Affective Neuroscience*, *8*, 410–417. http://doi.org/10.1093/scan/nss082

Wang, Y., Yang, L., & Wang, Y. (2014). Suppression (but not reappraisal) impairs subsequent error detection: An ERP study of emotion regulation's resource-depleting effect. *PLoS ONE*, *9*. http://doi.org/10.1371/journal.pone.0096339

Webb, T. L., Miles, E., & Sheeran, P. (2012). Dealing with feeling: A meta-analysis of the effectiveness of strategies derived from the process model of emotion regulation. *Psychological Bulletin*, *138*, 775–808. http://doi.org/10.1037/a0027600

Wegner, D. M. (1989). *White bears and other unwanted thoughts*. New York, NY: Viking/Penguin.

Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). A functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity*, *2*, 125–141. http://doi.org/10.1089/brain.2012.0073

Wierenga, C. E., Bischoff-Grethe, A., Melrose, A. J., Irvine, Z., Torres, L., Bailer, U. F., … Kaye, W. H. (2015). Hunger does not motivate reward in women remitted from anorexia nervosa. *Biological Psychiatry*, *77*, 642–652. http://doi.org/10.1016/j.biopsych.2014.09.024

Yamasaki, H., LaBar, K. S., & McCarthy, G. (2002). Dissociable prefrontal brain systems for attention and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 11447–11451. http://doi.org/10.1073/pnas.182176499

5 Curriculum Vitae

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EDUCATION

09/2012 – 10/2015	**University of Zurich**, Biopsychology & **University of Basel**, Social psychology: PhD thesis "Neural mechanisms of self-control exertion". Advisors: Prof. Dr. Malte Friese & Prof. Dr. Björn Rasch
09/2012 – 09/2015	**Swiss Federal Institute of Technology** & **University of Zurich**, Neuroscience Center Zurich: Fellow of the International PhD Program in Neuroscience
07/2012	Summer School **Dynamics of Consciousness** from the European Society for Cognitive Psychology (ESCOP), Zakopane, Poland: Participation in the summer school
09/2007 – 04/2011	**University of Zurich**: Master of Science in Psychology (lic. phil.). Major in Cognitive Neuroscience & Neuropsychology, Minors in Psychopathology & Human Biology
06/2009 - 09/2009	**Vivantes Psychiatry**, Berlin, Germany: Internship as a clinical psychologist
09/2006 - 07/2007	**University of Basel**: Studies in Philosophy, Biology, and Psychology
10/2005 - 04/2006	**Psychiatric University Clinics Basel,** Department of Depression, Sleep Medicine and Neurophysiology: Research internship
09/2003 - 04/2005	**University of Zurich**: Lower-level studies in Psychology
09/2003	**Rychenberg High School**, Winterthur: Graduation, Matura
08/2000 - 07/2001	**Brookfield Central High School**, Milwaukee, WI, USA: Language stay/exchange year during high school

PRACTICAL EXPERIENCE

10/2015 – 04/2016	**University of Zurich**, Biopsychology & **University of Basel**, Social psychology: Post-doctoral research fellow in a research project examining willpower and self-control with EEG
03/2014 – 03/2016	**Initiative Psychologie im Umweltschutz** (association for psychology in environmental issues), Zurich: Board member, volunteer work including maintenance of the website, organization and conduction of various workshops, co-organization of a conference with 150 attendees
04/2012 – 07/2012	**Life Science Communication**, Zurich: Tutor of an exhibition on functions and disorders of the nervous system and neuroscientific research
10/2008 – 10/2011	**University of Deusto**, Faculty of Psychology and Education, Spain, & **University of Zurich**, Institute of Industrial Organisational Psychology: Research assistant

05/2011 – 07/2011	**Adolescent Psychiatric University Clinic Zurich**: Civilian service, care of patients
11/2008 - 12/2010	**Swiss Federal Institute of Technology Zurich**, Institute for Behavioural Sciences, Research on Learning and Instruction: Research assistant

TALKS & CONGRESS ATTENDANCES

Congress attendances

01/2016	**Edmond & Lily Safra Center for Brain Sciences** (ELSC) Annual Retreat, Kibbutz Ein Gedi, Israel: Oral presentation "Neural mechanisms of self-control exertion"
03/2015	**Cognitive Neuroscience** (CNS) Meeting, San Francisco, CA, USA: Poster presentation „No effect of self-control exertion on amygdala reactivity and emotional memory"
09/2014	49th Congress of the **German Society for Psychology**, Bochum, Germany: Oral presentation „Wenn weisse Bären und Geld Selbstkontrolle beeinflussen"
04/2014	**Cognitive Neuroscience** (CNS) Meeting, Boston, MA, USA: Poster presentation „When white bears and money influence self-control"
05/2013	39th Congress "**Psychologie und Gehirn**" (Psychology and Brain), Würzburg, Germany: Poster presentation "Increased motivation counteracts depletion of self-control"
06/2009	13th Annual Meeting of the **Association for the Scientific Study of Consciousness** (ASSC), Berlin, Germany: Congress attendance
04/2009	2nd Symposium "**Hallucinations and Altered States of Consciousness in Philosophy and the Cognitive Sciences**" by ARTHEMOC and the French National Research Agency (ANR), Paris, France: Volunteer assistance during the congress

Invited talks

01/2016	**Conscious Lab** (Prof. Ran Hassin) & **Human Cognitive Neuroscience Lab** (Prof. Leon Deouell), The Hebrew University of Jerusalem, Israel: Oral presentation "Neural mechanisms of self-control exertion"
03/2015	**Consciousness & Metacognition Lab** (Prof. Hakwan Lau), UCLA, Los Angeles, CA, USA: Oral presentation „Studying self-control with fMRI"

GRANTS

11/2015	**Edmond & Lily Safra Center for Brain Sciences** (ELSC), The Hebrew University of Jerusalem, Israel: Competitive travel grant covering travel and accommodation to attend the 2016 ELSC Annual Retreat
05/2015	**EMDO foundation**, Zurich: CHF 20'000 for a research project on "Impacts of self-control exertion on cocaine consumption"
02/2015	**University of Zurich**, Department of Psychology: CHF 1'000 (Travel grant) to attend CNS Meeting 2015
02/2014	**Swiss Federal Institute of Technology** & **University of Zurich**, Neuroscience Center Zurich: CHF 1'000 (Travel grant) to attend CNS Meeting 2014

Review Work

02/2015	Ad-hoc reviewer for **Social Cognitive and Affective Neuroscience**

Teaching Experience

02/2015 – 08/2015	**University of Zurich:** Lecturer of the seminar "Neuroscience applied to clinical and social-psychological topics"
04/2013 – 06/2014	**University of Zurich:** Supervision of two master projects

Computer Skills

Matlab, SPSS, Mendeley
fMRI: SPM, Presentation Software
EEG: Brainvision Analyzer, LORETA